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FRONTISPIECE. Upper 4 and lower left 2: Now extinct Kaua'i 'O'o (*Moho braccatus*) in various attitudes. Lower right 2: The nearly extinct 'O'u (*Psittirostra psittacea*) in characteristic postures. Photographed July 1975 in the Alaka'i Swamp, Kaua'i by Robert J. Shallenberger except lower right by H. Douglas Pratt.

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REFLECTIONS ON A 1975 EXPEDITION TO THE LOST WORLD OF THE ALAKA'I AND OTHER NOTES ON THE NATURAL HISTORY, SYSTEMATICS, AND CONSERVATION OF KAUA'I BIRDS

SHEILA CONANT[1,4], H. DOUGLAS PRATT[2], AND ROBERT J. SHALLENBERGER[3]

ABSTRACT.—We observed, tape recorded, and photographed birds of the Alaka'i Plateau on Kaua'i, Hawai'i for one week during the summer of 1975. We observed all but one of the island's historically known species and compared the Alaka'i Plateau with the more accessible Koke'e area. Ours were the last studies before catastrophic changes in the Kaua'i avifauna and included many observations that cannot now be repeated. This retrospective report presents our findings in the light of subsequent events. Because our Alaka'i studies were seminal in the development of the current AOU classification of Hawaiian native passerines, we defend that classification against recent challenges and further refine it. The controversial genus *Hemignathus* is shown to be supported by a suite of synapomorphies of plumage, bill morphology, and vocalizations. We advocate removal of the 'Anianiau from *Hemignathus* and classify it as *Magumma parva.* Our studies of foraging behavior and vocalizations support the recent recognition of the Kaua'i 'Amakihi (*H. kauaiensis*) as a separate species and suggest that the 'Elepaio (*Chasiempis*) is best split into three species (*sclateri, ibidis,* and *sandwichensis*). Major hurricanes in 1983 and 1992 appear to have severely impacted Alaka'i bird populations with the subsequent extinction of the Kaua'i 'O'o (*Moho braccatus*) and possibly the Kama'o (*Myadestes myadestinus*), and the island population of 'O'u (*Psittirostra psittacea*). We report some of the last natural history observations on these species. Formerly adaptive strategies for storm survival, including taking refuge in valleys, are no longer effective because the lowlands are now infested with mosquito-borne avian diseases. The Puaiohi (*M. palmeri*), a ravine specialist, suffered less from the storms although its population remains perilously low. Other forest birds, especially the 'Akikiki (*Oreomystis bairdi*), show noticeable declines since 1975. We speculate that introduced organisms such as alien plants can have a deleterious effect on ecosystems by altering feeding methods of birds even in areas where the weeds do not occur. We caution against the overly conservative use of species-level taxa for setting conservation priorities on remote islands. *Received 24 October 1996, accepted 27 June 1997.*

In July 1975 we spent a week in one of Hawai'i's last strongholds for native birds, the fabled Alaka'i Swamp on Kaua'i. We were fortunate to find all but one of Kaua'i's historically known native bird species. At that time, we assumed that this relatively large wilderness area, under no obvious threat, would remain a refuge for endangered birds at least for the near future. Thus, although our observations contributed to subsequent publications, we published no general summary of our expedition. Time has shown that our optimism was naive; we made some of the last observations and tape recordings, and took some of the last (or only) photographs, of sev-

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eral species, and made the last natural history studies of several others under anything resembling "normal" conditions. We herein report numerous observations that will likely never be repeated and make comparisons with the current status of birds on Kaua'i. We interpret and amplify our 1975 observations with subsequent observations on Kaua'i birds made by the authors individually and with relevant unpublished observations of other naturalists that they have generously shared with us.

We also discuss the implications of our observations for ongoing systematic controversies, including some previously unpublished supporting details for Pratt's (1979) revision of the Hawaiian honeycreepers, the basis for the classification in widest use today (American Ornithologists' Union 1983, Sibley and Monroe 1990, Tarr and Fleischer 1995). We have made some refinements of Pratt's (1979) classification, which was "eclectic" (sensu Raikow 1985) but based on a cladistic analysis, to make it better reflect phylogeny.

Only a few major scientific studies of Kaua'i forest birds followed our expedition: the 1981 survey made as the final part of the landmark U.S. Fish and Wildlife Service population study (Scott et al. 1986), various studies by the U.S. Forest Service (C. J. Ralph and colleagues, unpubl. data), and several surveys by other state and federal wildlife agencies (e.g., Engilis and Pratt 1989; Pyle 1990, 1994; Telfer 1993). Several species declined noticeably between 1975 and 1981, and Hurricanes Iwa in 1982 and Iniki in 1992 severely reduced remaining bird populations in the Alaka'i (Engilis and Pratt 1989; Pratt 1994a; Pyle 1983, 1993b) apparently because the montane forest birds' historic habit of riding out severe storms in lowland valleys is now maladaptive, the valleys being infested with disease-carrying mosquitoes (Atkinson et al. 1993, Pyle 1993a, Pratt 1994a). Today, the endemic Kaua'i 'O'o and Kama'o (see species accounts) may both be extinct, and the 'O'u has not been certainly reported since Hurricane Iniki in 1992 despite diligent searches by competent biologists. Among other island endemics, the Kaua'i Nukupu'u barely survives (J. Jeffrey, pers. comm.), the Puaiohi is very rare (Pyle 1994; T. Snetsinger, pers comm.), and the 'Akikiki is proposed for listing as an Endangered Species (T. Pratt, pers. comm.). In view of these unexpectedly rapid changes, and because the Biological Resources Division, U.S. Geological Survey, has initiated a new research program to study Kaua'i's endangered birds as the century draws to a close (T. Snetsinger, pers. comm.), a report of our 1975 work is timely.

STUDY AREA AND METHODS

Our primary study site was within what is now the Alaka'i Wilderness Preserve. We were airlifted by helicopter to headwaters of the Halehaha Stream, near one of the late John L. Sincock's (Harrison et al. 1992) study areas we call "Sincock's Bog" (Fig. 1), late in the afternoon of 1 July 1975. Our flight was hampered by low-hanging clouds and fog, but the next morning dawned bright and clear, and such uncharacteristically dry weather prevailed for the rest of our stay until just before our departure on 8 July, when clouds and fog again closed in. Each night produced heavy dew.

RJS used a Nagra portable tape recorder and a Dan Gibson parabola; HDP used a Sony cassette recorder and an 46 cm Sony PBR-400 parabola. All recordings were later archived at the Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology, and some have been published (Hardy and Parker 1985; Pratt 1996). SC used binoculars and a stopwatch to record activity patterns and behaviors of several species. All 3 authors took numerous color photographs of birds, plants, and the habitat as 35 mm transparencies. A small series of specimens collected by HDP was deposited in the Museum of Natural Science, Louisiana State University.

The misnamed Alaka'i Swamp is actually a wet montane plateau mostly above 1000 m elevation spreading northwest from Mt. Wai'ale'ale, often considered the world's wettest spot, with mean annual rainfall of 1415 cm or 449 in. (Giambelluca et al. 1986). The plateau is deeply dissected by numerous forested ravines or canyons that feed into highly eroded Waimea Canyon, which drains to the south. The ridges between the streams can be broad and nearly flat, pocked in many places by open bogs (probably the origin of the "swamp" designation).

Our study area included a small (approximately 4 ha), open bog where the helicopter landed (Fig. 1). The surrounding dense rainforest was dominated throughout by 'ohi'a-lehua (*Metrosideros collina*). 'Ohi'a characteristically forms a dense canopy with numerous emergent snags (Fig. 2) that provide display perches for several native birds. The bright red brush-like 'ohi'a flowers, which lack petals, are the primary nectar source for several honeycreepers. The nectar collects in a cuplike calyx at the base of the red stamens so that nectarivorous birds must insert the bill deep into the inflorescence. The forest in the study area was very dense even at ground level and heavily overgrown with epiphytes. The epiphytic community in-

FIG. 1. Sincock's Bog as viewed from the air (upper) and from ground level (lower) with HDP in the foreground. Photos by RJS.

FIG. 2. Profile of forest canopy in the study area showing emergent 'ohi'a snags. Photo by HDP.

cludes abundant mosses and ferns as well as flowering plants.

Below the bog to the south the terrain sloped sharply to a rushing stream. In places, the banks were so steep that large 'ohi'a trees leaned over the stream almost horizontally. In other places, the streambed widened into relatively flat amphitheater-like areas that supported the growth of grass as well as small trees and shrubs. Such areas had obviously been scoured by debris during times of high water. With the help of Dr. C. H. Lamoureux, who worked from our photographs, we were able to identify many, but not all, of the dominant or common plants in the study area (Table 1).

For comparative purposes, we made a short visit to Koke'e State Park, an area just west of the Alaka'i swamp, immediately prior to our expedition. The park area differs from the heart of the Alaka'i in having much more koa (*Acacia koa*) among the canopy trees and in the presence of numerous alien plants and birds. The Koke'e region is served by many roads and trails and we have returned to it individually many times in the ensuing decades to monitor changes in Kaua'i's avian community. We mostly visited areas served by the Pihea Trail, Camp 10 (Mohihi) Road, and the Alakai Swamp Trail to the edge of the Alakai Wilderness Preserve (for maps and details see Pratt 1993).

THE AVIAN COMMUNITY

Through the 1960s, Kaua'i was considered unique among the Hawaiian Islands in having lost none of its historically known bird species (Richardson and Bowles 1964) and the Alaka'i Plateau remained a seldom-visited wilderness. Birds in general were abundant in our study area, and native species far outnumbered aliens. Most native birds appeared to have just finished breeding. We saw few fledglings, but recently fledged immatures of several species were numerous. Except for the Kaua'i 'O'o, the Kama'o, and possibly the 'O'u, the passerines we observed did not appear to be defending breeding territories. Rather they ranged widely through the area; the species noted near our campsite changed on a daily basis. Also, few species were singing territorial songs; we recorded mostly call notes. Probably the best season for observing breeding activities in the Alaka'i would be April through June, although the peak of nesting may vary from year to year.

SPECIES ACCOUNTS

The following codes are used in this section: RE = resident, endemic Hawaiian species; RK = resident, species endemic to Kaua'i Island; RI = resident indigenous

TABLE 1. Major plant species identified in the study area, listed alphabetically within different forest strata. (Plant names follow Wagner et al. 1990).

Scientific name	Hawaiian name	Flowers	Fruit
Trees			
Cheirodendron sp.	'olapa		+
Metrosideros collina	'ohi'a-lehua	+	
Myrsine sp.	kolea	+	+
Pelea sp.	'alani	+	
Tetraplasandra sp.	'ohe	+	
Shrubs			
Broussaisia arguta	kanawao	+	+
Cibotium sp.	hapu'u	no notes	
Clermontia spp.	'oha		+
Dubautia paleata	na'ena'e puakea	+	
Rubus hawaiiensis	'akala		+
Scaevola glabra	'ohe naupaka	+	
Vaccinium calycinum	'ohelo kau la'au		+
Vaccinium dentatum	'ohelo	no notes	
Herbs and Epiphytes			
Adenophorus sp.	unknown	no notes	
Astelia sp.	pa'iniu	+	
Carex sp.	unknown	no notes	
Dianella sandwichensis	'uki 'uki	+	+
Drosera anglica	mikinalo	+	
Freycinetia arborea	'ie'ie	no notes	
Korthacella remyana var. *wawrae*	hulumoa	+	+
Lycopodium cernum	wawae 'iole	+	
Lycopodium serratum	unknown	+	
Nertera granadensis	unknown		+
Psilotum sp.	moa	no notes	
Smilax sandwichensis	hoi kuahiwi	+	
Viola kauaensis	poke hiwa	+	+

breeding species; A = alien breeding species. Federally recognized Endangered Species are noted as such.

*White-tailed Tropicbird or Koa'e-kea (*Phaethon lepturus dorotheae*), RI.*—We saw two individuals flying over bog at about 13:00 8 July, as we awaited our helicopter pickup. Tropicbirds are numerous in canyons and valleys throughout Kaua'i and nest in Hanapepe Valley south of our study area (HDP pers. obs.).

Hawaiian Duck or Koloa (Anas wyvilliana), RE, endangered.—RJS flushed one individual from the stream bed just below camp. The bird was in a wide part (about 15 m) of the stream where it was probably standing on a rock or in a dense growth of sedge (*Carex* sp.). The duck is also present in low numbers and may nest along Kawaikoi Stream in the Koke'e area. Although Hawaiian Ducks concentrate in lowland wetlands such as the taro fields at Hanalei (Pratt 1993), they also nest in the mountains (Berger 1981).

*Red Junglefowl or Moa (*Gallus gallus*), A.*—HDP flushed one bird from the ground in the low forest north of the bog on 4 July, and found an abandoned large nest on the ground in the same area. We did not hear any dawn "crows" from our campsite. The unusually large numbers of these birds that congregate around buildings in Koke'e State Park are apparently lured there and maintained by food handouts from visitors.

*Short-eared Owl or Pueo (*Asio flammeus*), RI.*—Solitary individuals were observed soaring, possibly hunting, a few meters above the tree tops once or twice each day, usually in the afternoon or early evening. The owl is also uncommon in the Koke'e region. Although historically regarded as an endemic subspe-

FIG. 3. Juvenile Kaua'i 'Elepaio. Photo by HDP.

cies, this cosmopolitan species may be a post-Polynesian colonizer of the Hawaiian Islands (Olson and James 1991).

*Kaua'i 'Elepaio (*Chasiempis sclateri*), RI.*—In 1975, only one species of 'elepaio was recognized, with subspecies on Kaua'i (*C. sandwichensis sclateri*), O'ahu (*C. s. gayi,* later emended to *C. s. ibidis* by Olson 1989a), and Hawai'i (*C. s. sandwichensis*). Subsequently, the Hawai'i form was shown to exhibit intra-island variation at the subspecies level, with at least three forms recognizable (Pratt 1980). The striking plumage differences of the Kaua'i and O'ahu forms clearly qualify them as "megasubspecies" (sensu Amadon and Short 1976), and they are unquestionably "phylogenetic" species (sensu Cracraft 1983). Olson and James (1991; see footnote to Table 1) recognized three species of *Chasiempis,* but whether they consider them biological or phylogenetic species is unclear.

Our work on Kaua'i combined with observations on other islands (Conant 1977, Pratt 1980) supports the recognition of three biological species of *Chasiempis.* The adult Kaua'i 'Elepaio is the plainest and the only one with a gray dorsum. Juveniles are mostly rufous, without the white rump and wing-bars of the adults, and closely resemble juveniles of the O'ahu form in color but seem subjectively to be subtly different (more rotund, less linear) in shape (Fig. 3). Plumage dimorphism is lacking in adults on Kaua'i and O'ahu, but Hawai'i adults are strongly dichromatic (Pratt 1980, Pratt et al. 1987).

The variations in tempo and pitch of the vocalizations of the Kaua'i 'Elepaio have not been thoroughly investigated, but the repertoire is qualitatively distinguishable from those of the O'ahu and Hawai'i forms (Pratt 1996). E. VanderWerf (pers. comm.) recently found that O'ahu 'Elepaio respond differentially to playback of their own vocalizations and those of Hawai'i birds. Similar studies with the Kaua'i 'Elepaio are ongoing. All 'elepaio are bold and inquisitive, but the Kaua'i birds are particularly so, the juveniles more than adults. Juvenile Kaua'i 'Elepaio approach humans closer, sometimes perching within arm's reach, and follow them farther than do 'elepaio on other islands. Both age categories respond readily to imitations of their whistled songs and calls as well as "spishing." We saw several fledglings including one whose rectrices were only 1–2 cm long. This suggests that the breeding season ends about the same time as that of the O'ahu 'Elepaio (Conant 1977, Sherwood 1995), but earlier than that of the Hawai'i representative (Bollinger and Bollinger 1987).

Ecologically, all three 'elepaio species are forest birds, but as their islands differ, so do the birds' respective habitat preferences. We observed both adult and immature Kaua'i 'Elepaio frequently every day in our study area, and found them also common at Koke'e. They are restricted to the higher and wetter parts of the island (Scott et al. 1986) and have not undergone any obvious decline since 1975 (Engilis and Pratt 1989, Walther 1995). In contrast, the O'ahu 'Elepaio has declined strikingly during the same period (Williams 1987, Pratt 1994a, Conant 1995) and is now rare, with a fragmented distribution restricted primarily to relatively mesic valleys at middle elevations (VanderWerf et al. 1997). It has apparently always been more common in drier, mid-elevation forests (Bryan 1905). On Hawai'i, the intra-island variation in plumage color is correlated with rainfall (Pratt 1980).

Apparently the three *Chasiempis* were first "lumped" by Bryan and Greenway (1944), who gave no data to support the change in status; and subsequent authors, until Olson and James (1991), accepted that taxonomy by default. We believe a return to recognition of three species, with *C. sandwichensis* having three intra-island subspecies, provides a more meaningful and balanced taxonomic treatment that better reflects the observed geographic

variation. Because the three forms are allopatric, biological species limits must be assessed by inference. Our observations, as well as those of VanderWerf (in press), show that the striking plumage differences are backed up by potential behavioral and ecological isolating mechanisms. We can discern no reason, other than the general similarities reflected at the generic level, to consider them conspecific.

*Kama'o (*Myadestes myadestinus*), RK, endangered, possibly extinct.*—This larger of the two Kaua'i solitaires (Pratt 1982), then called the Large Kaua'i Thrush, was not uncommon in the study area during our visit. As many as seven individuals could be seen simultaneously perched on emergent 'ohi'a snags in the forest surrounding the bog above our camp in the early morning and at dusk. They perched upright with the tail down. From inside the forest, Kama'o were difficult to see, but we heard their songs and calls throughout the day in the vicinity of the campsite. They gave two different calls, one a cat-like rasp and the other resembling the sound of a police whistle. These calls are similar to, but distinguishable from, calls of the 'Oma'o (*M. obscurus*) of Hawai'i. The song of the Kama'o is entirely different from that of the Hawai'i bird and resembles closely the song of Townsend's Solitaire (*Myadestes townsendi*) of western North America, with some of the tonal quality of the song of the Slate-colored Solitaire (*M. occidentalis*) of Mexico. These song differences were among early indications that the Kama'o and 'Oma'o were separate species, later confirmed by Pratt's (1982) playback experiments on Hawai'i using recordings made during our Alaka'i visit. The song of the Kama'o is long and complex with an ethereal, echoing, and cascading quality. A typical singing performance ended with the bird rising on its wings, hovering over the forest while singing constantly, and then abruptly diving into the trees. Pratt (1982) presented sonagrams of the two call types and the song, and recordings of all three have now been published (Pratt 1996). What was once Kaua'i's most abundant forest bird (Munro 1944) may well be extinct; it has not been seen since Hurricane Iniki (Walther 1995; T. Snetsinger, pers. comm.). A February 1989 survey by the Hawaii Division of Forestry and Wildlife (DFW) reported two "probable" sightings, but no birds were heard (Pyle 1989). That report noted that on a 1985 DFW survey many Kama'o were heard. DFW again surveyed the Alaka'i Swamp in 1993, and two "brief but inadequate" possible sightings of Kama'o were reported (Pyle 1993b).

*Puaiohi (*Myadestes palmeri*), RK, endangered.*—Our first sighting of this species occurred at dusk on 3 July. A single bird flew from the forest underbrush and perched silently above our camp site. In the fading light we could see the bird was a heavily spotted immature, with a few down feathers still clinging to the head. The pink feet were evident as the bird perched upright facing us. Later, HDP saw two other individuals, both adults. One was located by slowly searching out the source of a dry, toneless hiss that proved to be the call note. The bird was perched almost motionless on a mossy stump under a concealing clump of vines and shrubs at the upper rim of a small ravine. In posture, this individual resembled the bird seen previously, as it sat bolt upright rather in the manner of a tyrannid flycatcher. It remained for some minutes in this position, uttering its calls at about 10-s intervals. It then flew to the end of a small stump that extended from a high bank over the stream. Again, the bird remained motionless for some minutes and then flew away into the forest. The third individual was glimpsed briefly as it flushed from concealment in a small (ca. 5 m) 'olapa (*Cheirodendron trigynum*) tree that grew in a wide, flat area of the streambed (Fig. 4). These observations demonstrate that this species is extremely difficult to detect where it occurs, and thus may have been more common in the Alaka'i than the few published observations would indicate. All of our sightings were in or near a deep, protected stream valley, as have been other observations (Ashman et al. 1984, Kepler and Kepler 1983, Pyle 1984), whereas most of the Kama'o we observed were near the more exposed ridge-top bog. The smaller solitaire appears to be a ravine specialist. This may partly explain why the Puaiohi, although historically much the rarer of the two Kaua'i thrushes (Perkins 1903), has weathered the two recent hurricanes much better than its larger relative. A very small population of Puaiohi persists in the Alaka'i (T. Snetsinger, unpubl. data) and is the subject

FIG. 4. An open area of stream bed on Halehaha Stream where HDP flushed a Puaiohi. Photo by HDP.

of intense observation and possible recovery actions by federal agencies and The Peregrine Fund. These ongoing studies have already discovered a larger than expected population (Pyle 1996) in the Koai'e Stream area (almost directly between Koke'e and our 1975 study site) where two nests were found about a decade ago (Ashman et al. 1984, Kepler and Kepler 1983).

*Melodious Laughing-thrush (*Garrulax canorus*), A.*—RJS briefly saw one bird in low, dense vegetation above the campsite. On Kaua'i, this bird is found in dense mesic and wet forests of both native and introduced plants. It is very secretive and almost always seen near the ground. Its loud song is the best indication of its presence. Although we have no record of vocalizations in our field notes, HDP later noticed the song in the background of one of his tapes.

*Japanese White-eye (*Zosterops japonicus*), A.*—White-eyes were present in the area but were greatly outnumbered by native birds. We saw only a few small groups. In contrast, they were common to abundant in the Koke'e area. This introduced species has become the most abundant forest bird on Kaua'i (HDP, pers. obs.; Scott et al. 1986).

*Kaua'i 'O'o or 'O'o'a'a (*Moho braccatus*), RK, endangered, possibly extinct.*—On 2 July we awoke to the song of the 'o'o (06:15). Shortly after the dawn chorus ceased and the sun was up, a single 'o'o appeared near our campsite and provided our first look. Interestingly, the bird did not visit us on subsequent mornings, indicating that it may have deviated from its usual feeding route to "check us out" that first day. The song (for recordings see Pratt 1996) is a series of loud, clear melodious whistles with a "tune" reminiscent of the song of the Western Meadowlark (*Sturnella neglecta*). Its tone quality is distinctly meliphagine, however, with a haunting, echoing quality, and is surprisingly similar to portions of the song of the Tui *(Prosthemadera novaeseelandiaee)* of New Zealand (for an example of the latter, see Gunn and Gulledge 1977). Other portions of the Tui song sound remarkably like the unrelated drepanidine 'I'iwi (discussed below). The Kaua'i 'O'o's song is

TABLE 2. Percentage of time devoted to 7 activities of 2 Kaua'i 'O'o during 61 minutes and 36 seconds of observation.

Activity	Percentage of time
Feeding at flowers	55
Inactive perching	29
Preening	9
Flying or hopping	3
Singing	3
Insect gleaning[a]	<1
Territorial chasing[b]	<1

[a] We feel this value is somewhat low based on many other untimed hours of observation.
[b] The pair was defending an apparent feeding territory, primarily against 'I'iwi and 'Apapane.

much more complex than those of the other species of *Moho* (Perkins 1903), but includes two-note phrases that probably resemble the "oh-oh" for which the birds were named. Each day birds sang at 10–20 min intervals until about 10:30, when song became less frequent. Duetting by the pair was frequent throughout the day. A sharp two-note whistle, which can be heard in the second cut of this species presented by Pratt (1996), appeared to be an alarm or alert call-note.

On 3 July we located an apparent feeding territory of a pair of Kaua'i 'O'o downstream from our camp. It included several large, heavily flowering 'ohi'a trees from which the pair excluded all other birds, a size-based hierarchy similar to that reported on Maui (Carothers 1986) and Hawai'i (Carpenter and MacMillen 1976). We surmised that the birds had several such feeding areas or territories that they patrolled systematically because they would leave this area for 20–40 min at a time, usually flying off to the northeast and returning northwest. This foraging pattern is consistent with observations of "trap-line" feeding in East Maui. There, both the 'I'iwi and the 'Akohekohe (*Palmeria dolei*) revisit blooming 'ohi'a trees with a regular cyclicity of about 20–35 min (HDP pers. obs.). Probably the cycle is set by the rate of nectar production of *Metrosideros*. Besides taking nectar from 'ohi'a flowers the birds foraged for insects from masses on the larger branches and among small branches and foliage. One bird ate small black 'olapa berries. Hart (1978) also reported a bird eating 'olapa fruits, and saw a bird taking insects from moss clumps. The birds moved quickly and decisively through the trees often holding the tail cocked in a nearly vertical position (Frontispiece). SC timed various behaviors of two birds with a stopwatch, and used data to characterize activity patterns and foraging behavior (Tables 2 and 3).

We were able to confirm the presence of only one pair of Kaua'i 'O'o, although on one occasion we may have heard a third individual call in the distance while both birds were under observation. By 1981, only a single known pair survived, possibly the same birds we observed (Scott et al. 1986). The female of the last known pair was not found after Hurricane Iwa (Pyle 1983), and the male was last seen in 1985 (Pyle 1989). The last report of this species was that of Cynthia and James

TABLE 3. Foraging behavior of two Kaua'i 'O' during 47 minutes and 11 seconds of observation (data recorded only while birds were feeding).

Vertical canopy occupation		Horizontal canopy occupation	
Height (m)	Percent time	Zone[a]	Percent time
2–4	18	Inner	14
4–7	11	Center	<1
>7	71	Outer	86

Movement Patterns During Feeding	
Percent time moving	57
Percent time stopped (feeding pause)	43
Rate of feeding pauses	3.9 pauses/min
Rate of movement (not including feeding pauses)	2.1 m/min
Rate of movement (including feeding pauses)	1.2 m/min
Average distance between feeding pauses	0.3 m

[a] Canopy zones: Inner = within 1 m of the central axis of tree; Outer = within 1 m of outermost crown foliage; Center = between inner and outer.

FIG. 5. 'O'u (*Psittirostra psittacea*) male (l.) and female (r.). Photos by RJS. See also Frontispiece.

Krakowski, who heard an 'o'o calling on 28 and 29 April 1987 (Pyle 1987). A survey by state agency biologists in February of 1989 found no 'o'o, and the report speculated that the birds were "now probably gone" (Pyle 1989). They have not been reported since and are undoubtedly extinct, their loud vocalizations being difficult to overlook.

*Northern Cardinal (*Cardinalis cardinalis*), A.*—SC heard one bird singing the morning of 8 July for our only observation. Northern Cardinals were and remain common to abundant at Koke'e, where the forest is more disturbed. In general, they are one of the more widespread introduced birds throughout the Hawaiian Islands, but are rare in primary forest (Pratt et al. 1987).

*'O'u (*Psittirostra psittacea*), RE, possibly extirpated.*—We located several pairs of 'O'u near our campsite (we estimated about one pair per 4 ha). They were usually heard before they were seen, giving their characteristic, loud, mellow, upslurred call-note, but were difficult to locate because the call is ventriloquial. SC saw males singing on several occasions, but was unable to record the song, a complex canary-like performance, starting with two downwardly inflected notes, followed by a short, upslurred note, and a descending warbling trill and ending with a low downwardly inflected note of about the same frequency as the second note. HDP also noted a single short song, comprising whistles and a trill, that he was unable to record but transliterated as *feee-tooo-ter-wheet-wheet-wheet-wheet-wheet-feee-tooo.* When the males sang, they fluffed all the body plumage and flapped their wings clumsily. The bill was open during singing and the body quivered slightly.

All the birds we saw sat quietly or moved slowly and heavily in upper portions of dead snags or on high exposed perches. As a result, most of our photographs, which appear to be the only ones ever taken of this species, are strongly back-lighted and fail to show the birds' colors to good effect. Their perching posture was distinctively horizontal, with the tail held slightly up but not cocked. They appeared rather pot-bellied (Fig. 5, Frontispiece). Although we spent several hours watching various individuals, HDP saw only one bird actually feed, apparently taking nectar from an 'ohi'a flower.

A Kaua'i 'O'u population in the low hundreds in the late 1970s was apparently decimated by Hurricane Iwa in 1982 (Pyle 1983, Engilis and Pratt 1989). The last published Kaua'i sightings were made on 16 and 17 February 1989 (Pyle 1989). The population on Hawai'i has likewise dwindled, and there have been no recent reports of 'O'u on that island. The 'O'u is on the brink of extinction, if any yet survive.

*Kaua'i 'Amakihi (*Hemignathus kauaiensis*), RK.*—This was the scarcest of the "common" honeycreepers in our study area, and was observed on only three occasions. HDP saw an individual near the camp on 6 July, and above it on 8 July. The first bird was clinging to a vertical 'ohi'a trunk and picking over the bark, very much the way the 'Akikiki forages. SC and RJS observed a bird feeding on 'ohe naupaka (*Scaevola glabra*) flowers, which are 4–6 cm long. To obtain nectar, the bird in-

serted its head into the bright yellow tubular corolla, rather than piercing a hole at the flower base as we have seen other Kaua'i 'Amakihi do at morphologically similar flowers. It also took insects from around flower bases.

At Koke'e, with more koa, the Kaua'i 'Amakihi was common in 1975 and remains so today (HDP, pers. obs.). We attribute its rarity in the study area to the absence of koa. In 1975, the Kaua'i 'Amakihi was regarded as one of four subspecies of 'Amakihi (*H. virens*), although Bock (1970) considered its bill size differences sufficient to separate it specifically from other 'amakihis. The bill is much larger than those of other 'amakihis, with little or no overlap in measurements (Fig. 6). Interestingly, the recently split O'ahu 'Amakihi (*H. chloris*), the Kaua'i bird's apparent closest relative (Tarr and Fleischer 1994), shows the least approach or overlap of all. Birders inexperienced on Kaua'i may fail to appreciate the degree of difference and consequently misidentify a Kaua'i 'Amakihi as a Nukupu'u (discussed below). Therefore, reports of Nukupu'u on Kaua'i should be regarded with some skepticism unless accompanied by unequivocal details.

Our 1975 observations and subsequent studies (Pratt 1979) found potential isolating mechanisms of the Kaua'i 'Amakihi among ecological and behavioral characters. The bird spends much more time picking prey from the bark of trees and less time feeding among leaves and flowers than other 'amakihis. Raikow (1974) found such distinctive foraging behavior to be innate. The typical call of both the Common 'Amakihi and the O'ahu 'Amakihi is a short, buzzy or mewing note rather similar to the call of the Blue-gray Gnatcatcher (*Polioptila caerulea*) of eastern North America. The Kaua'i 'Amakihi also utters such a note, but only occasionally. Its typical call is a loud upslurred chirp (Pratt 1996), sometimes indistinguishable from calls of 'Anianiau, 'Akeke'e, and 'Akikiki, all of which join mixed flocks on Kauai. All 'amakihis sing short trills (Pratt et al. 1987, Pratt 1996), but the loudest notes of the Kaua'i bird's trill usually drop in pitch whereas those of the other forms remain level. The repeated elements of the Kaua'i bird's trill appear simpler in sonagrams, and the song also usually has a distinctive introductory note that is not

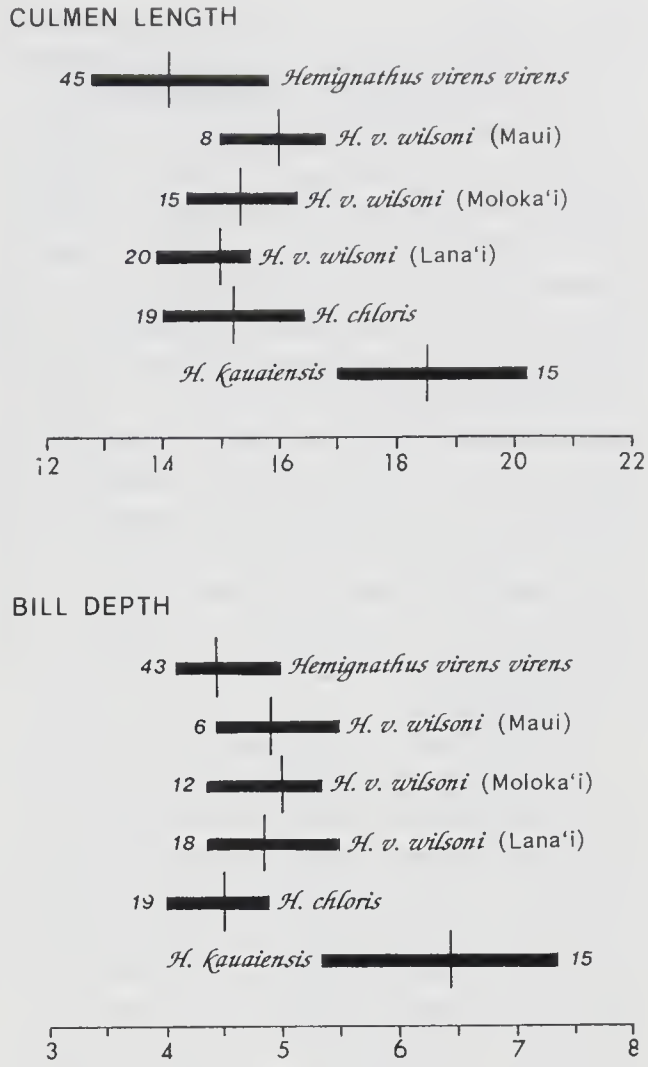

FIG. 6. Bill measurements of 'amakihis from various islands, adapted from Pratt (1979). Means are indicated by long vertical lines, ranges by horizontal bars. All measurements in millimeters. Number of specimens examined at ends of bars.

present in 'amakihi songs from other islands (Pratt 1996). Individual trills of *H. virens* typically last about two seconds, but those of *H. kauaiensis* are about a half-second shorter. Further, although the songs of all species are variable, the Kaua'i bird seems to have a wider range of variation that includes trills on a nearly level pitch. This observation may explain why birds on Hawai'i that responded to songs of conspecifics from Maui failed to respond to playback of Kaua'i songs, whereas Kaua'i birds responded equally to either tape (Pratt 1979). Kaua'i birds may have recognized the level-pitched trills as within their range of variation, but Hawai'i birds did not recognize the descending trills from Kaua'i.

Based on the large suite of potential isolating mechanisms and a level of morphological

differentiation comparable to species-level rank in other passerines, Pratt (1979) and Pratt et al. (1987) recognized the Kaua'i 'Amakihi as a species, as did James and Olson (1991), on the basis of osteological studies and Johnson et al. (1989) and Tarr and Fleischer (1994) based on biochemical studies. The American Ornithologists' Union (1995) has now recognized the split. The Kaua'i 'Amakihi's taxonomy is rather convoluted because its generic placement has been controversial. The correct specific epithet depends on whether one places the 'amakihis in *Hemignathus* or in some other genus. The specific epithet of the Kaua'i 'Amakihi is *stejnegeri* in any genus other than *Hemignathus,* where that name is preoccupied (Olson and James 1988). Pratt (1989a) proposed *kauaiensis* as a replacement in *Hemignathus.*

Historically, *Hemignathus* was used either for the 'akialoas, with the bill greatly elongated, and the nukupu'us, with a short mandible and elongated maxilla, together (Amadon 1950), or for the 'akialoas alone with the nukupu'us segregated as *Heterorhynchus* (e.g., Perkins 1903). Olson and James (1995) pointed out that both names are based on the same type species; they restricted *Hemignathus* to the nukupu'us and named the genus *Akialoa* based on the Hawaiian name for those birds. Pratt (1979) was the first to place the similarly plumaged but short-billed 'amakihis in *Hemignathus,* although R. C. L. Perkins (*in* Wilson and Evans 1890–99) also considered the 'amakihis closer to the 'akialoas and nukupu'us than to the 'akepas (*Loxops*) with which Amadon (1950) grouped them. Olson and James (1995) denigrated those (e.g., American Ornithologists' Union 1983, Sibley and Monroe 1990, Tarr and Fleischer 1995) who followed Pratt's (1979) classification, stating wrongly that it was adopted "without any consideration having been given to its merits" (Olson and James 1995:374). Because the observations we began in 1975 in the 'Alaka'i Swamp were seminal in the development of Pratt's (1979) taxonomy, we herewith reconsider its merits, as compared to the classification of the Olson/James team (see also Pratt 1994b).

Pratt's (1979) classification was based on the literature dealing with tongue morphology, breeding biology, myology, and osteology as well as firsthand investigations of plumage coloration and ontogeny, sexual dimorphism, vocalizations, foraging behavior, and ecology. Qualitative characters such as bill shape and plumage pattern were the most useful in delimiting genera, whereas such characters as tongue morphology and, surprisingly, vocalizations proved more useful as indicators of higher relationships. Numerous recent studies have shown that the traditional prejudice against the use of plumage color in alpha taxonomy (as stated by Amadon 1950:166 and clearly evident in many other works of that era) has no justification. In the two other most frequently cited avian examples of adaptive radiation, the Vangidae (Langrand 1990) and Geospizinae (Lack 1968, Grant 1986), plumage pattern is as good a predictor of relationships as any external character, and is much more useful in delimiting genera than bill size or length, a character that Amadon (1950) apparently considered pre-eminent and reiterated in his critique of Pratt's (1979) revision (Amadon 1986). Members of Pratt's *Hemignathus* have sharply pointed downcurved bills that are dark colored with a pale base to the mandible. Adults are dull green above and more or less yellow below, with narrow dark lores. Sexual dimorphism is pronounced, with males larger, longer billed, and always yellower than females. Juveniles resemble adult females but have pale wing-bars (retained in adult females of *H. chloris*). The bill shape and most of the suite of color characters differ from the ancestral condition in Drepanidinae (Raikow 1977), are not found among the Carduelinae (for illustrations of all species see Clements 1993), and can only be regarded as synapomorphies. Except for the 'Anianiau (discussed below), which we no longer consider to belong to the genus, the various *Hemignathus* are so similar in plumage at any age and in either sex that the bill would have to be seen to confirm identification in the field (Pratt et al. 1987). Some other avian genera (*Calidris, Nectarinia,Toxostoma,* and *Geospiza* come to mind) exhibit a similar range of variation in bill length and shape.

James and Olson (1991) based their alternative classification primarily on cranial osteology, particularly the feeding apparatus, because the postcranial anatomy of Hawaiian honeycreepers is so uniform as to provide lit-

tle phylogenetic information (Raikow 1977). Because they were classifying numerous recently found subfossils, their focus on osteological characters was understandable, and they stated forthrightly (James and Olson 1991:23) that they had not attempted a phylogenetic analysis. In their most recent revision, Olson and James (1995) recognized the genera *Akialoa* and *Hemignathus* (nukupu'us only) with the 'amakihis being placed in *Loxops* along with the 'akepas and the Hawai'i Creeper ("*L.*" *mana*). In so doing they reconstituted Amadon's (1950) *Loxops,* minus the three species of *Paroreomyza* and the 'Akikiki (discussed below).

Amadon's (1950) *Loxops* is probably the most extreme example of alpha-level taxonomic over-lumping in the annals of avian systematics. It included one species of crossbilled 'akepa, now shown to be at least two biological species (Pratt 1989b); four subspecies of curve-billed 'amakihi now regarded as three species (Tarr and Fleischer 1994); the nearly straight-billed Greater 'Amakihi (*Viridonia* sensu stricto) which may be related to the newly discovered fossil genus *Aidemedia* (James and Olson 1991); the 'Anianiau (*Magumma,* discussed below) which may not be closely related to the 'amakihis after all (Tarr and Fleischer 1995); and a "species" Amadon called "the Creeper" now regarded by all authors as five species in two (Pratt 1992b) or three (Olson and James 1982, James and Olson 1991) possibly unrelated genera! The only conceivable character these birds have in common is a short bill (Pratt 1979). The removal of four of Amadon's "subspecies" of "creeper" from his *Loxops* does not make the genus any more tenable. It has no defining synapomorphies or even any general similarities to unite its disparate members. Olson and James (1995:375) stated misleadingly that unpublished genetic studies by R. Fleischer support their treatment ". . .with the proviso that the 'akialoas have not yet been analyzed and that the amakihis may need to be further split." They fail to mention that Tarr and Fleischer's (1995) recently published findings lend equal support to Pratt's treatment, depending on which of two algorithms one follows, and even then the genetic studies say nothing about where generic limits should be set among closely related groups. Obviously, biochemical studies do not always resolve systematic disputes.

A classification compatible with both views would recognize the genus *Viridonia* for the 'amakihis with *Loxops, Akialoa,* and *Hemignathus* as separate genera. We consider this a counsel of despair, however, because it would turn back the taxonomic clock a century, when nearly every species of Hawaiian honeycreeper had its own genus. Such a classification is devoid of phylogenetic information and ignores demonstrated synapomorphies that cluster the three curve-billed green drepanidine groups. The only way to taxonomically recognize that cluster is to consider it a genus with *Viridonia, Hemignathus,* and *Akialoa* (but not *Loxops*) as subgenera because the entire drepanidine taxon, once considered a family, may be only a tribe (Sibley and Monroe 1990; James and Olson 1991).

*'Anianiau (*Magumma parva*), RK.*—This bird was common, and we observed it frequently every day taking nectar and probably insects from 'ohi'a flowers. Birds foraged in the tops of flowering trees along with 'Akeke'e and 'Apapane, but we saw no interspecific aggression. Occasionally the 'Anianiau foraged much lower, particularly among kanawao (*Broussaisia arguta*) plants. On 8 July SC observed a single individual taking nectar by inserting its bill into the tubular corollas of 'ohe naupaka (*Scaevola glabra*) flowers. When 'ohi'a is not in full bloom, the 'Anianiau is an active and agile insectivore, seeking its prey among smaller branches and leaves (Raikow 1974, HDP pers. obs.). In its movements and postures it resembles a wood-warbler (Parulinae).

HDP saw an adult feeding a fledgling barely able to fly on 8 July. July may be the last month of the breeding season. Hart (1976) saw a male giving courtship displays before a female on 26 May 1976. Berger et al (1969) suggested that the nesting season of this species extends from mid-February to late June. We heard no singing by this species in our study area, but had learned the song, a trill of doublets or triplets, during our prior visit to Koke'e. The typical call note is a 2-syllable *tew-weet,* the first note low, the second rising. Other calls resemble those of Kaua'i 'Amakihi, 'Akeke'e, and 'Akikiki. The 'Anianiau remains as common today as it was in 1975,

despite an apparently temporary reduction in numbers following Hurricane Iniki (HDP, pers. obs.). It is by far the most abundant of the "green" honeycreepers in the Koke'e area.

When first described, the 'Anianiau was placed in the genus *Himatione* (which, at the time, included the 'amakihis and the "creepers") but was thought to be closer to the creeper group than to the 'amakihis (Wilson and Evans 1890–99:xxi). As the species became better known it was placed with the 'amakihis in *Chlorodrepanis* (Perkins 1903), and some authors even used the English name "Lesser Amakihi" for it. In his eclectic classification, Pratt (1979) uncritically accepted the 'amakihi relationship and placed the 'Anianiau in *Hemignathus*. Although it is a yellow-green bird that resembles the 'amakihis behaviorally, close examination reveals that the 'Anianiau lacks the defining synapomorphies of *Hemignathus*. Sexual dimorphism is much less pronounced than in 'amakihis, nukupu'us, and 'akialoas, and the dark lores are totally lacking. The bill is short, only slightly downcurved, and flesh-colored with a dusky culmen. A cladistic reinterpretation of Pratt's (1979) classification would place the 'Anianiau in its own monotypic genus between *Loxops* and *Hemignathus*. The phylogeny of those three genera cannot be resolved on the basis of present knowledge. This taxonomy is consistent with Tarr and Fleischer's (1995) genetic studies (although not predicted by them), whichever algorithm one follows, as well as with those of Johnson and coworkers (1989). Mathews (1925) proposed the generic name *Magumma* as a replacement for the preoccupied *Rothschildia* so that a name would be available if the 'Anianiau was ever placed in its own genus.

*Kaua'i Nukupu'u (*Hemignathus lucidus hanapepee*), RK, endangered.*—A single bird, observed by SC, perched on the top of an 'olapa tree for about 30 seconds at 19:00 on 4 July. This subspecies is extremely rare, and, at the time, had been seen on only two occasions (Sincock *in* Haley 1975) since its rediscovery in 1960 by Richardson and Bowles (1964). The USFWS forest bird survey in 1981 failed to find any Nukupu'u, but 1985 saw a flurry of credible sightings in several localities (Pyle 1985a, b). Reports in the Koke'e area by isolated observers (Pyle 1985b, 1988, 1992) have lacked sufficient details for unequivocal elimination of Kaua'i 'Amakihi (discussed above). The Nukupu'u differs from the 'amakihi in having the head paler (bright yellow in males, duller in females) without a contrasting darker crown and a darker, thinner-based bill (Pratt et al. 1987) and it virtually never feeds in flowers (Perkins 1903).

Because searches immediately following Hurricane Iniki failed to find any Nukupu'u (Pyle 1993c), many feared that it shared the fate of the Kama'o. However, on 10 May 1995, while conducting bird surveys along the Mohihi-Waialae Trail near Koai'e Stream, T. L. C. Casey (pers. comm.) heard a short whistle, resembling one call of the Maui Parrotbill (*Pseudonestor xanthophrys*), that turned out to be given by a Nukupu'u. Her notes include a detailed description of the bill as ". . .longer and slimmer than [that of] a Kaua'i 'Amakihi, particularly at the base where the [bill of the] Kaua'i 'Amakihi is quite heavy." She identified the bird as a female on the basis of its dull yellow head and noted that it ". . .spent several minutes foraging through branches of 'ohi'a and 'olapa, working each branch upwards from side to side." Casey watched the bird for about three minutes as it foraged with a mixed-species flock of small birds that included 'Anianiau and Kaua'i 'Amakihi. This observation is consistent with Perkins' (1903) report that Nukupu'u often accompany such flocks.

In the same general area, Casey saw a male Nukupu'u on the morning of 22 June 1995. It gave a call similar to that of the previous bird but showed a much brighter yellow head. Later the same day at the same locality, J. Jeffrey (pers. comm.) observed a female Nukupu'u for approximately 30 seconds. His descriptions, particularly of the bird's behavior are definitive. He noted that when foraging, "the bird used its bill to rip open the thin bark and wood and probe with the upper bill [showing] that the maxilla was longer than the mandible and that the mandible was also curved downward. To feed, the bird appeared to push the maxilla into or under the bark or soft wood then pull back on the maxilla while using the mandible as a fulcrum, tearing the bark or wood." Although these sightings seem to in-

dicate the presence of at least one pair at this locality, other observers (D. Kuhn, J. Lepson, pers. comms.) subsequently failed to find any Nukupu'u there. This species' long term survival at very low numbers is quite remarkable.

*Kaua'i 'Akialoa (*Hemignathus stejnegeri*), RK, endangered, extinct.*—This was the only historically known Kaua'i forest bird that we failed to see during our 1975 expedition. Following the 1960 rediscovery of this species (Richardson and Bowles 1964), the only detailed published report of it was that of Huber (1966) of a sighting in 1964 in the same general area as those of 1960. His description of the bird's awkward use of its extremely long bill as it fed among 'ohi'a flowers is convincing. The Kaua'i 'Akialoa was both an insectivore that probed among epiphytic mosses, lichens, and ferns and a nectarivore that fed on deep lobelioid flowers as well as the more open flowers of 'ohi'a (Perkins 1903, Richardson and Bowles 1964). Although details have not been previously published, P. L. Bruner (pers. comm., Pratt et al. 1987) saw a Kaua'i 'Akialoa in 1969. An undergraduate and beginning ornithologist at the time, he was taken to a spot by local hunters and shown the bird, but could not reconstruct the exact locality. Apparently it was on land owned by Gay and Robinson, because his guides were former employees of that corporation, and thus it was not the same place as the previous sightings. In conversations with HDP in 1971, Bruner described the bird's head-down probing of the undersides of large branches and reported being surprised by the bird's very large size, an attribute that would not have been apparent to him from the popular literature of the time (e.g., Peterson 1961, which gives a deceptively small rendering). Only later, upon examining specimens, did HDP come to realize how much bigger the 'akialoa was than other green honeycreepers on Kaua'i. We are convinced that Bruner was the last person to see a Kaua'i 'Akialoa.

Huber's (1966) report contains an enigmatic description of the 'akialoa's call. He saw the bird in the same tree as an 'O'u that was characteristically sitting so motionless that he failed to notice it at first. He stated that both birds were calling and that the notes were identical except that one was upslurred, the other downslurred, and he could not remember two years later which was which! As noted earlier, we heard many 'O'u whistles that were upslurred. Thus, we were intrigued by a downslurred whistle, recorded by both RJS and HDP, we heard late in the afternoon of 2 July 1975 northwest of Sincock's Bog. The author of this call was too far away in dense forest for us to see it (the sun was setting at the time), and we never heard the downslurred call again. Did we, in fact, hear the "last" Kaua'i 'Akialoa? The question remained open until 1989, when A. Engilis (pers. comm.) heard a similar call and saw that it was uttered by an 'O'u. On that basis, and because Huber may well have heard the call of an unseen 'O'u and attributed it to his 'akialoa, Pratt (1996) presented our downslurred call as "'O'u, Call 2." Noteworthy is that Perkins (1903) described no similar note for the Kaua'i 'Akialoa but instead described its calls as distinct but intermediate between those of its congeners, the Kaua'i 'Amakihi and the Nukupu'u. Nevertheless, we will probably always be haunted by our unseen whistler.

*'Akikiki (*Oreomystis bairdi*), RK, proposed endangered.*—Although we observed 'Akikiki (formerly called Kaua'i Creeper) every day, they were not as common as 'Elepaio, 'Akeke'e or 'Apapane. The 'Akikiki forages by creeping along larger branches and takes prey from the bark surfaces, crevices, lichens, and mosses. One bird spent three minutes taking insects from the bases of 'ohi'a inflorescences (SC, pers. obs.). HDP noted several family groups consisting of immatures and a pair of adults. The young were fully feathered and seemingly adept at foraging but still begged. Immatures are distinguished by white "spectacles" (Fig. 7). We heard no songs from the 'Akikiki, only call notes, which resemble those of the Hawai'i Creeper (*Oreomystis mana*) but are a bit louder (Pratt 1992b). Since 1975, the 'Akikiki has declined catastrophically. A 1990 expedition to Sincock's Bog failed to find any (Pyle 1990), although subsequent searches have found them in the area in low numbers, even after Hurricane Iniki (Pyle 1993b). None were found by Walther (1995) in his 1994 surveys west of the Alaka'i Wilderness Preserve, although D. Kuhn (pers. comm.) and tour groups led by HDP have consistently found them through 1995 at the Kawaikoi Stream crossing on the Alaka'i

FIG. 7. Juvenile 'Akikiki (*Oreomystis bairdi*) showing distinctive white "spectacles," Alaka'i Swamp, 1975. Photos by RJS.

Swamp Trail, the most reliable locality outside the preserve (Pratt 1993). Recently, 'Akikiki have again been found in encouraging numbers along the Mohihi-Waialae Trail (Pyle 1996). Appropriately, the 'Akikiki is being considered for listing as an Endangered Species (T. Pratt, pers. comm.).

As with other insectivorous Hawaiian honeycreepers, the classification of the 'Akikiki has been somewhat controversial. Pratt (1979) placed *Oreomystis* with the other thin-billed insectivores, excluding the enigmatic and possibly nondrepanidine (Pratt 1992a, Tarr and Fleischer 1995) *Paroreomyza,* in the tribe Hemignathini, but a cladistic analysis supported its independent derivation from a finch-like ancestor (Pratt 1992b). Johnson and coworkers (1989), whose analysis of drepanidine phylogeny substantially and irreconcilably disagreed with those of other biochemical systematists on many points, recommended that *Oreomystis* and *Paroreomyza* be placed in one tribe and all other drepanidines in another. Tarr and Fleischer (1995) found *Oreomystis* to be allied with the finchlike Psittirostrini and not closely related to *Paroreomyza.* We believe transfer of *Oreomystis* from the Hemignathini to the Psittirostrini is justified, even though it would become the only insectivorous genus in that assemblage, assuming Pratt's (1979) placement of the Maui Parrotbill (*Pseudonestor xanthophrys*) with the Hemignathini (contra AOU 1983) is correct. The question of whether *Oreomystis* is monotypic (Olson and James 1982, 1991) or includes the Hawai'i Creeper as *O. mana* (Pratt 1992b) will be discussed elsewhere (Pratt in press).

*'Akeke'e (*Loxops caeruleirostris*), RK.*— This species, formerly called Kaua'i 'Akepa, was common in the study area and provided daily observations, but none was singing at the time. They kept to the outer canopy where feeding movements were difficult to discern in detail. 'Akeke'e often appeared among inflorescences of 'ohi'a, but we could not confirm whether they actually took nectar. Subsequent research has revealed that the 'Akeke'e forages almost exclusively in 'ohi'a (Lepson and Pratt in press), unlike its sister species, the 'Akepa (*L. coccineus*), which forages in a wide variety of trees and shrubs (Pratt 1989b, Conant 1981, Lepson in press).

The bills of the two *Loxops,* with their slightly crossed tips, have been the subject of much speculation as to the manner of their use. Based solely on their study of the birds' strongly asymmetrical jaw musculature and skeleton, Richards and Bock (1973) presented a lengthy and highly detailed scenario of how the bill might be used. Both methods they described involve a 90° rotation of the head during feeding, a twisting motion that should be obvious to an observer, yet none of our observations in 1975 or subsequent ones of both species involved any such movement, nor has it been reported by any other observers. When foraging among leaf buds, both the 'Akeke'e and the 'Akepa look just like birds feeding at inflorescences, i.e., the head is held still and all action is accomplished by the bill and tongue. Benkman (1989) described the feeding of the 'Akeke'e at Pu'u o Kila in the Koke'e area in some detail: no head-twisting occurs; the bird parts the scales of 'ohi'a leaf buds by gaping and laterally abducting the lower mandible after the closed bill has been inserted. HDP confirmed Benkman's observations at the same locality in October 1992 and also observed the action of the tongue, which Benkman (1989) did not report. After the leaf scales were pushed apart, the tongue was extended vertically down into the crevice, then withdrawn into the bill with a small linear object (presumably an insect larva) entangled at a 90° angle in the brush-like tip. On 24 September 1995 HDP observed identical feeding movements by several 'Akeke'e in the upper Kawaikoi Stream valley along the

Alaka'i Swamp Trail. To date, no aspect of Richards and Bock's (1973) scenario has been confirmed by field observation.

In February 1993, HDP made an enigmatic observation of 'Akeke'e feeding behavior at the northern edge of the Alakai Wilderness Preserve: a male 'Akeke'e twice bit the edge of a mature 'ohi'a leaf, pinking the edge with two v-shaped indentations about 1 cm apart. The leaf could not be examined closely but through 10 × 40 binoculars appeared healthy and without any insect damage. Whether the bird ate the leaf sections could not be determined. Among HDP's 1995 observations were several "nibbles" at leaf edges, but no sections were removed. Folivory in general is very rare in birds (Munson and Robinson 1992) and has previously been reported in only one Hawaiian honeycreeper, the Laysan Finch (*Telespiza cantans,* Conant 1988).

*'Apapane (*Himatione sanguinea*), RE.*—This was the most common bird in our study area. Numerous adults and immatures were taking nectar from 'ohi'a flowers in the tree tops. Songs and call notes were given virtually all day. This was one of the two species that the Kaua'i 'O'o chased from a grove of heavily flowering 'ohi'a trees (probably the 'o'o's feeding territory). 'Apapane were abundant at Koke'e in 1975 and remain common today but were noticeably reduced by Hurricane Iniki. One seen in a ravine in Kalaheo, a lowland locality directly south of Sincock's Bog, by members of a tour group led by HDP six weeks after the storm provided modern confirmation of historical accounts of displacement of montane birds by storms (Pratt 1994a).

*'I'iwi (*Vestiaria coccinea*), RE.*—We saw this bird daily, but not frequently. Solitary individuals took nectar from 'ohi'a, *Clermontia* spp., and *Scaevola glabra.* We did not see it gleaning for insects amongst stems and foliage, as it may do when nectar is scarce. 'I'iwi, as well as 'Apapane were the target of feeding territory aggression by Kaua'i 'O'o. When taking nectar from flowers of *Clermontia* and *Scaevola,* 'I'iwi invariably pierced a hole in the base of the long tubular corollas characteristic of these plants. This feeding method contrasts with earlier observations such as that of Spieth (1966) and contravenes the seemingly obvious and often-cited evolutionary relationship between the bills of Hawaiian honeycreepers and the flowers they feed upon (Givnish et al. 1995, Lammers 1995, Patterson 1995). It clearly amounts to nectar-robbing because the bird avoids contact with the flower pistil. This anomaly leads us to speculate that this habit may be a recently learned feeding behavior influenced by introduced flowers with flower structures that evolved with different pollinators. Similar behavioral modification has been reported among Australian nectarivores (McCulloch 1977). Henshaw (1902) observed that 'I'iwi on Hawai'i had learned to pierce the "spur" of nasturtiums to reach the nectar, and Perkins (1903) reported Hawai'i 'Amakihi feeding on long lobelioid flowers that "they have learnt to pierce at the base, at least in certain localities." The flowers of the introduced South American passionflower *Passiflora mollissima* , known locally as banana poka, are too long and too straight for the 'I'iwi's curved bill, so the birds must pierce the corolla at its base to reach the base, as we have frequently seen them do. When in heavy bloom, these choking vines attract large assemblages of birds with the 'I'iwi predominating. Other species that frequent banana poka include Kaua'i 'Amakihi, 'Anianiau, 'Apapane, and Japanese White-eye. Whether the smaller-billed species are capable of piercing the large and relatively tough banana poka corollas or simply take advantage of holes made by 'I'iwi is not known. Such feeding assemblages were conspicuous at Koke'e in 1975, but the alien plant had not yet penetrated the heart of the Alaka'i. Nevertheless, banana poka may have had an insidious impact even in areas remote from infestations. Many large flowers native to Hawaiian forests, including representatives of such disparate families as Campanulaceae (Givnish et al. 1995, Lammers 1995), Malvaceae (Funk and Wagner 1995), and Goodeniaceae (Patterson 1995) in which flowers are not usually curved, have curved corollas and other structural modifications for feeding, and presumably pollination, by native birds. By "teaching" birds to rob nectar without pollinating flowers, banana poka and other alien plants may have broken the evolutionary link between Hawaiian plants and their bird pollinators. Thus, alien plants could be damaging

native ecosystems in a particularly devious way.

The voice of the 'I'iwi is highly distinctive compared to those of other drepanidines. It includes metallic screeches, dissonant reedy notes, bell-like notes, clicks, and humanlike whistles delivered in a measured, seemingly random cadence quite unlike the canarylike songs of drepanidine finches and the simple warbles and trills of the Hemignathini. Other members of the Drepanidini, though they share some of the 'I'iwi's tonal qualities, have much more "conventional" songs. Remarkably, the 'I'iwi's song bears a strikingly close resemblance to portions of the song of the aforementioned New Zealand Tui (see Kaua'i 'O'o account). In fact, one could produce a reasonable facsimile of the Tui song by splicing together pieces of the songs of the 'I'iwi and the Kaua'i 'O'o! None of these songs are much like the songs of meliphagids of central Polynesia (*Foulehaio carunculata, Gymnomyza* spp.). Why the songs of two unrelated Hawaiian birds should resemble so closely that of a bird that lives thousands of kilometers away is fertile ground for speculation. One possible explanation is that the song of the 'I'iwi developed as a response to food territoriality by as yet unknown Hawaiian meliphagids.

*Nutmeg Mannikin (*Lonchura punctulataa*), A.*—HDP saw three birds in Sincock's Bog on 8 July, having heard one calling earlier in the week. Although primarily found in lowland open habitats, Nutmeg Mannikins are commonly seen along trails in the Koke'e region and are the most likely of Kaua'i's introduced estrildids to be found in forest openings.

CONCLUSION

Our 1975 experience in the Alaka'i wilderness, viewed in two-decade hindsight, teaches several important lessons for biologists and environmentalists. Because it retained a relatively intact avifauna into the 1970s, biologists of the time were comparatively complacent with regard to both research and conservation on Kaua'i. Whereas Maui and Hawai'i were the subject of major research and conservation efforts in the 1970s, Kaua'i's forests held the long-term attention only of John Sincock, and it was the last of the islands to be surveyed systematically (Scott et al. 1986). Although major preserves were established by the federal government and The Nature Conservancy of Hawaii in forests on Maui, Moloka'i, and Hawai'i, Kaua'i saw only the belated designation of the Alaka'i Wilderness Preserve by the State of Hawaii. We cannot fault authorities for such actions; we, too, considered Kaua'i "safe" when compared to other islands that appeared to have more pressing concerns. The sudden collapse of Kaua'i's avifauna was a surprise. During the same period, Guam experienced an equally sudden ecological catastrophe that was also unexpected and rather mysterious (Pratt et al. 1979, Savidge 1987, Jaffe 1994). Neither island was perceived to be in imminent danger in the early 1970s, and both experiences show that island avifaunas can quite literally be here today, gone tomorrow. We now know that island avifaunas worldwide are mere remnants of what was present before the influence of humans (Olson 1989b; Steadman 1995), but these geologically rapid extinctions were slow compared to recent insular avian disasters. Any small-island endemic might well be considered inherently endangered. Although in the past HDP argued against listing locally common island endemics as Endangered Species (Pratt et al. 1979), we now believe that those who set conservation priorities should use different criteria for island versus continental species. That insularity, in and of itself, greatly increases any species' vulnerability can no longer be disputed.

We further believe that conservationists should revise their view of nominal island subspecies. Some conservationists (e.g., Hazevoet 1996) have suggested that the new "phylogenetic" species concept (Cracraft 1983), in which all distinctive island forms would be considered species, would better serve their purposes. However, such practical considerations are largely irrelevant to the ongoing philosophical debate in ornithology over species concepts (see Zink and McKitrick 1995 for a review). In our view, conservationists should work to save all distinctive island populations whatever species concept ornithologists ultimately adopt. We predict that most such populations will ultimately be shown to be good biological as well as phylogenetic species. In many cases, the requisite data necessary to shift the burden of

proof to the lumpers is available even in the original taxonomic revisions, which only need to be reinterpreted in the light of modern insight. In other cases, recent observations of vocalizations and ecology can help in the reassessment of species limits as we have done herein for several Kaua'i forms.

The "species only" policy of Collar et al. (1994), although understandable given the size of the problem, is unfortunate. The Kama'o, which was considered a subspecies of the 'Oma'o (*Myadestes obscurus*) until Pratt (1982) showed it to be a full biological species, is a case in point. By the time the new classification was officially adopted (AOU 1985), the population was so low that little could be done to save it. In 1975, biologists had far more concern for the Puaiohi, yet today the historically rarer thrush survives while the Kama'o apparently does not. A captive breeding program begun in 1975 might have gotten the species through the recent hurricanes, but none was even contemplated for a bird that was "only" a remote island subspecies.

Other conservation lessons from our observations include the findings that alien species on islands may have deleterious effects in previously unforeseen ways and that survival strategies that worked well in a pristine environment can become maladaptive in damaged ecosystems. Our studies also show that even seemingly superficial observations of island birds are important and should be published; we can never know when a given study may be the last. Most oceanic islands are much less frequently visited by ornithologists than Kaua'i. Gaps in the ornithological literature of 30 to 50 years are not uncommon for remote islands. Even a short interlude on a seldom-visited island can provide important data, and both scientists and recreational birders should neither overlook opportunities to make such observations nor denigrate the results as too superficial to be of value. Simply knowing whether a given species was present on a certain date may prove critical. Because islands are extremely useful natural laboratories for evolutionary and ecological studies, preservation of their avifaunas is particularly important and must be addressed immediately. Procrastination means extinction.

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Frontispiece. Margaret Morse Nice (1883–1974). Reproduced from her autobiography (Nice 1979) "Research is a passion with me" with permission of the publisher.

Wilson Bulletin, 110(1), 1998, pp. 25–27

Wilson Ornithological Society Establishes Margaret Morse Nice Medal

EDWARD H. BURTT, JR.[1]

> "On March 26 I . . . banded a very important individual—my first Song Sparrow—later called Uno. He owned the territory next to our house and on May 22 I found his nest with three eggs, two of which hatched on May 28 and 29. For five days I spent a total of 18 hours watching the family. Uno's mate was evidently an experienced bird for she fed more than he did during four hours on the 29th, but after that he outdid her record. . . . the two babies were carried off by some enemy the night of June 2 and so ended my observations on Song Sparrows in the spring of 1928 except for my becoming acquainted with Uno's spirited neighbour, later dubbed 4M, and my recording in words and symbols of four of his distinctive songs" (Nice 1979:91).

So began Margaret Morse Nice's landmark study of the Song Sparrows (*Melospiza melodia*) nesting in the floodplain below her home on the Olentangy River just north of Columbus, Ohio. Over the next eight years she pioneered the use of bands to mark individual birds and follow the lives of each one. She described the melodic variations used by different male Song Sparrows and how variations were shared among neighbors. Later she would explore song learning and behavioral development in hand-raised Song Sparrows. Her individually marked birds enabled her to explore site fidelity of males, females, and offspring and the social interactions among neighbors. Through her study of Song Sparrows she introduced many of the concepts of European ethology to American ornithologists (Nice 1939a).

In August of 1935, Margaret Nice began writing "Studies in the life history of the Song Sparrow" (1937). On 25 June 1936 her journal entry reads:

> "It has taken one solid year of work writing it up, . . . Have done almost no field work for a year, no trips . . . very little other writing . . . Well, it's an achievement" (Nice 1979:151).

Indeed it was. Of this first volume, "Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow," Jean Delacour wrote:

> "In its form, this book is a model of clarity; in its substance, it is perhaps the most important contribution yet published to our knowledge of the life of a species" (Delacour 1937:656).

In 1943 the second volume (Nice 1943) was published with the following evaluations:

> "This treatise is far superior to anything of the kind that has been previously attempted. Many of the chapters . . . are complete treatises in themselves with enough meat in them to fill separate volumes" (Mayr 1944:60).

> "No other life-history study combines such rich scholarship with such keen field work" (Hickey 1943:231).

In 1943 her achievement was recognized by the American Ornithologists' Union which awarded Margaret Morse Nice its prestigious Brewster Medal given to the author of ". . . the most important work relating to the birds of the Western Hemisphere . . . over the last six years." On the rim was engraved "Margaret Morse Nice Life History of the Song Sparrow."

Margaret Morse Nice was born on 6 December 1883 in Amherst, Massachusetts. Her father, Anson Daniel Morse, was a professor of history at Amherst College with a deep love of the wilderness and a devotion to gardening. Her mother, Margaret Duncan Morse, a graduate of Mount Holyoke Seminary, taught her the names of wild flowers during Sunday afternoon walks. In 1891, at the age of seven, Margaret received her first bird book. In 1896 she wrote and published a small booklet, "Fates and fortunes of Fruit-acre birds." She graduated from Mount Holyoke College in

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1906 and, a year later, entered Clark University as one of only two women graduate students. Her master's thesis (Nice 1910) was the first comprehensive study of diet in the Northern Bobwhite (*Colinus virginianus*). In 1908 she married Blaine Nice, also a graduate student at Clark University and in 1913 they moved their family to Norman, Oklahoma where he had accepted a faculty position at the University. From 1913 to 1927 Margaret Morse Nice worked on her "Birds of Oklahoma" (1931), often with the help of her daughters. In 1927 the family moved to Columbus, Ohio where Blaine had accepted a professorship at The Ohio State University. In 1936, shortly after finishing the first volume of her life-history of the Song Sparrow, she and Blaine moved to Chicago where he was to head the Departments of Physiology and Pharmacology at the Chicago Medical School.

Although a landmark among ornithological studies, Margaret Morse Nice's contributions to ornithology are not limited to her studies of the Song Sparrow. She joined the American Ornithologists' Union in 1907, attended her first meeting in 1908, and in 1920, at the 38th Stated Meeting, she was the only woman to present a paper. The next year she joined the Wilson Ornithological Society. She attended her first Wilson meeting in 1927 when she reported (1930) on the nesting of Myrtle Warblers (*Dendroica coronata*). In 1933 she founded the literature review section of Bird-Banding (now Journal of Field Ornithology). Over the next nine years she wrote 1800 reviews, most summarizing and commenting on ariticles written in foreign languages, of which she read five fluently. In 1935 she was elected Second Vice-President of the Wilson Ornithological Society and succeeded to its Presidency in 1937, the first woman to preside over one of the world's major ornithological societies. Also in 1937 she was elected a Fellow of the American Ornithologists' Union, only the second woman so honored. She published a popular account of her field work, "The Watcher at the Nest" (1939b), a major review of territoriality (1941), a review of incubation periods of North American birds (1954), and an important synthesis of our knowledge of behavioral development in precocial birds (1962). She was made an honorary member of the German Ornithological Society and a Corresponding Member of the Royal Hungarian Institute of Ornithology. In 1955 Mount Holyoke College and in 1962 Elmira College awarded her honorary Doctor of Science degrees. Perhaps Dean Richard Bond of Elmira College best summarized the career of Margaret Morse Nice when he stated:

> "She used the outdoors near her home as her laboratory and common species of birds as her subject. In so doing, she joined the ranks of the eminent ornithologists of all time, who saw so much in what appeared common to so many" (Nice 1979:262–263).

The Wilson Ornithological Society is pleased to establish the Margaret Morse Nice Medal in recognition of her scientific creativity and insight, her concern for the education of young and amateur ornithologists, and her leadership as an innovator and mentor. The medal honors a lifetime of contributions to ornithology. The recipient will be invited to review her or his contributions and their significance to ornithology and science in general at the opening plenary lecture of the annual meeting of the Wilson Ornithological Society. The recipient will also be invited to publish the substance of those remarks in the Wilson Bulletin.

The first recipients of the Margaret Morse Nice Medal are Elsie C. and Nicholas E. Collias whose research on hormones and behavior, the mechanisms, development and evolution of nest-building in the Village Weaver, the role of family integration and dominance in avian social behavior, and, most recently, the genetics of egg color exemplify the scientific and creative excellence Margaret Morse Nice embodied and the Wilson Ornithological Society wishes to honor.

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SEEKING TO UNDERSTAND THE LIVING BIRD
The 1997 Margaret Morse Nice Lecture

NICHOLAS E. COLLIAS[1,2] AND ELSIE C. COLLIAS[1]

For over 50 years the classic study by Margaret Morse Nice on the life and behavior of the Song Sparrow (*Melospiza melodia*) has given a basic orientation and ideas for research to investigators of the natural behavior of birds. She made the first detailed, long-term study of the behavior of wild birds color-banded for individual identification (Nice 1933, 1934). She had an excellent education and the two volumes of her monograph on the Song Sparrow (Nice 1937, 1943), one on populations, one on behavior, are written from the viewpoint of basic biological problems, enlivened by her profound curiosity about the life of birds. Mrs. Nice was a firm believer in confirming for herself any important published fact about bird behavior, which is the reason why research was a passion with her (Nice 1979). In this spirit of direct scientific inquiry, we wish to present some highlights of our own research.

We have spent much of our lives trying to understand the biology of avian behavior, especially the function, causes, ontogeny and evolution of social behavior at the physiological, individual and population levels of organization (N. Collias 1991). The first part of this presentation will be given by Nicholas, the second by Elsie, but we have generally worked together.

Let me briefly introduce ourselves. My early childhood was in Chicago Heights, then a small town, where my family lived on the edge of town. Soon after learning to read, I discovered in the local library "The Burgess Bird Book for Children" (Burgess 1919) with its magnificent color plates by Louis Agassiz Fuertes. These plates gave me names for the common birds that I encountered in the nearby fields and woods. I vividly recall my first glimpse of a bluebird in an orchard. It seemed as if a fragment of the blue sky had fallen and was flying about on the back and wings of a bird, an impression still fresh after three-quarters of a century. I was not then aware that anyone in my world had any real interest in birds aside from myself and Peter Rabbit, the hero of the bedtime stories by Thornton W. Burgess. It was far from my thoughts that anyone could make a living watching birds, until years later when a scholarship to the University of Chicago made possible for me a career in zoology and ornithology.

The situation was different for Elsie, some of whose ancestors, like those of Margaret Nice, arrived in New England in the 1600s. Eventually, Elsie's family settled in Tiffin, Ohio, near the Sandusky River. Her parents encouraged her early interests in nature and taught her the local birds. Her father, Heath K. Cole, was a lawyer with a strong interest in the natural sciences. Elsie, before she started school, developed a great interest in insect life, and readily prevailed on her father to make her an insect net. She eventually donated a substantial insect collection to Heidelberg College, her alma mater in Tiffin. After a year in research on malarial mosquitoes with the United States Public Health Service, Elsie went back to finish her Ph.D. work in zoology at the University of Wisconsin, where we met. Our friendship included getting up well before dawn to watch the prairie-chickens dance near Plainfield, Wisconsin, where we were two of the thousands of guests that Fran and Fred Hamerstrom introduced to these fascinating birds over the years. After Elsie and I were married we did our research together on birds.

UNIVERSITY OF CHICAGO (1937–1942). HORMONES AND BEHAVIOR

Mrs. Nice and her family moved to Chicago in 1936 and bought a house near the University of Chicago where I was a student, and we became friends.

My research career began after graduation in 1937 when Professor W. C. Allee of the University of Chicago zoology department hired me as his research assistant to work on the effects of hormones on the peck order of

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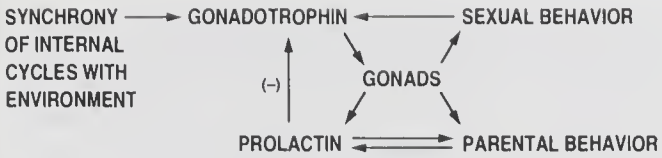

FIG. 1. Interactions between hormones and behavior in the control of breeding behavior in doves and pigeons. Inhibition indicated by minus (–) sign. (After N. E. Collias 1952 and Collias and Collias 1984).

hens. Testosterone and estradiol had been isolated in pure form in 1935 (Marrian 1950). In chickens, the cock's testes secrete testosterone, the hen's ovary secretes testosterone, estradiol, and progesterone (reviewed in Collias and Collias 1984).

We found that ovariectomized hens injected with testosterone became more aggressive and rose in the peck order, some from the bottom to the top (Allee et al. 1939). Ovariectomized hens injected with the female sex hormone, estradiol, became sexually receptive but they did not rise in the peck order (Allee and Collias 1940).

Rank in the peck order is decided by fighting or passive submission at the initial encounter of each pair of birds. Success in initial encounters between normal hens is correlated with larger comb size, a specific indicator of testosterone. In my Ph.D. thesis, using the path coefficient method of Professor Sewall Wright and with his advice, I found that a much greater percentage of the variance in success was determined by differences in comb size than in body weight or in previous success, while molt had a depressing effect on success (N. Collias 1943).

Mrs. Nice, who was president of the Chicago Ornithological Society from 1939 to 1941, invited me to speak before that society, and I spoke about hormones and behavior of birds as a self-regulating system with positive and negative feedback relations. Ten years later (N. Collias 1950), I reviewed the literature on the subject in some detail.

Figure 1 shows the interactions between the environment, hormones, and behavior. Originally it was based largely on pigeons and doves (N. Collias 1952), but indications now are that it may apply to many other birds as well. This figure was confirmed by a review of more recent literature in 1984 (Collias and Collias 1984), and I think is consistent in a general way with more current evidence as critically reviewed in 1996 by Buntin, who also brings out the variation between different species of birds.

There are two general phases in the breeding cycle of birds, a sexual phase stimulated by pituitary gonadatrophin and gonadal steroid hormones, and a parental phase dominated by pituitary prolactin. The gonadal hormones stimulate pair formation, nest building and copulation. Male Ring Doves stimulate the females to lay eggs, as I found in a controlled experiment (N. Collias 1950), confirming Wallace Craig's demonstration of the same thing in 1911. Gonadal hormones, together with the mate, nest and eggs, also help bring about onset of incubation.

In 1935, Oscar Riddle and his colleagues discovered that prolactin injected into laying hens stimulates maternal behavior, i.e., incubation and care of chicks. Sitting on eggs in turn stimulates prolactin secretion. However, a hypophysectomized male pigeon that I injected with estradiol thereupon paired with a normal female and helped her incubate her eggs for over a month, showing that prolactin is not absolutely necessary for parental behavior (N. Collias 1950), although it normally stimulates it (Buntin 1996). By inhibiting gonadotrophin, rising prolactin levels help end the sexual phase of breeding.

Today, comparative endocrinology of wild birds in nature is a relatively new and flourishing field of research, made possible by such techniques as radioimmunoassay of minute hormone levels in the blood, a technique for which Rosalyn Yalow of New York received a Nobel Prize in 1977. For many species of birds it has now been amply confirmed that a sexual phase dominated by steroid sexual hormones is succeeded by a parental phase more or less dominated by prolactin (Buntin 1996), for example, in the Song Sparrow (Wingfield and Goldsmith 1990).

UNIVERSITY OF WISCONSIN (1947–1951). ANALYSIS OF FAMILY INTEGRATION AND VOCAL COMMUNICATION

I served as Instructor in Zoology at the University of Wisconsin for four years. After 3 and 1/2 years in the Army in World War II, I was more interested in family life than in peck

orders. Like Mrs. Nice, who as a young girl raised chickens, my first acquaintance with details of individual bird behavior was with chickens. The focus of my research at Wisconsin was on family integration, and this led to an interest in vocal communication.

Family integration and leadership.—When a baby chick is lost, cold, hungry, thirsty, or in pain, it utters distress cries (chirps). When the chick is returned to its mother or to its siblings, or the specific distress is relieved, the chick promptly switches to pleasure notes (twitters). To a newly hatched chick, the mother hen is a complex of warmth, physical contact, clucking sounds, and within about an hour, also a moving object. Loss of any one of these maternal stimuli may cause the chick to give distress cries and when the stimulus is restored it moves toward the source of the stimulus, normally the mother hen (N. Collias 1952).

In its social development the chick goes through a series of stages (N. Collias 1952, 1962):

(1) Initial predisposition to response to certain key stimuli.
(2) Self-reinforcement of these responses during an early sensitive period (filial imprinting).
(3) Increasing social discrimination and recognition of individuals.
(4) Social independence, exploration and social maturity with age and experience. Chicks on being isolated from companions give progressively fewer distress cries as they get older.

The first two stages depend especially on genetically determined predispositions, the last two stages involve learning to a greater extent.

In 1935, Lorenz graphically described filial imprinting of newly hatched Greylag Geese (*Anser anser*) that followed him about. In 1950, I confirmed in a controlled experiment that the day of hatching was a sensitive period in which chicks begin to follow the parent and that responsiveness fell off precipitously in succeeding days if first exposure to parental stimuli is delayed (N. Collias 1952).

Leadership among small chicks of a brood may contribute to family integration. Among recently hatched chicks of about the same age (3–4 days) some specific individuals may lead the other chicks to maternal clucking (from a speaker) or to a source of warmth (warm lamp) in a cool room. A chick that forges very far ahead of the others, however, may utter distress cries and is likely to turn back to rejoin its companions. A good leader has both independence, and empathy with companions or young ones (N. Collias 1952).

Social guidance by the parent bird or other individuals enters into every stage of social development, and climaxes when birds learn traditional migration routes from experienced individuals, as has been indicated for geese and cranes (Lishman 1996). There has been a tremendous amount of work on social learning of the song of songbirds, including the Song Sparrow (Hauser 1996, Kroodsma and Miller 1996), and this is related to species identification.

A basic code of vocal communication.—During World War II, The Bell Telephone Company invented the sound spectrograph, a machine that makes precise visual pictures of sounds and gives a harmonic analysis of sounds (Potter 1945). This machine has revolutionized the study of animal communication. Professor Martin Joos, a linguist at the University of Wisconsin was one of the first to obtain a sound spectrograph for scientific studies. In 1953, he and I presented the first spectrographic study of the repertoire of vocal signals of an animal, the domestic fowl (Collias and Joos 1953).

We found that the spectrogram of chick pleasure notes emphasizes ascending frequencies, that of distress cries descending frequencies. The two opposed vocal signals apparently express states of security and insecurity, respectively. This is an example of what Darwin (1872) called the principle of antithesis, or that opposite states of mind as he put it, are accompanied by antithetical motor expressions. The different vocal signals of chickens, including those of their wild ancestor, the Red Junglefowl (*Gallus gallus*) are composed of elements that can be arranged in antithetical pairs, in effect a code (N. Collias 1987):

(1) Pitch rises or falls.
(2) Low versus high pitch.
(3) Clear, distinct tones versus harsh sounds where harshness is defined

spectrographically as harmonic streaks combined with a wide and superimposed spread of frequencies.
(4) Brief versus long notes.
(5) Soft (low amplitude) versus loud notes.

In different vocal signals, the first element in pairs 2 to 5 above tends to attract chicks, the second element usually repels them. Different combinations of elements produce different vocal signals. For example, soft, low-pitched and brief notes as in clucking of a mother hen attract baby chicks, as was confirmed by experiments with comparable artificial sounds (Collias and Joos 1953). But harsh, loud, high-pitched and long sounds strongly repel them and cause chicks to rush to shelter. In the case of adults, loud, harsh and high-pitched sounds are also alarm cries, but harsh and lower-pitched sounds are threats. Quite similar elements in the vocal signals of the Village Weaver (*Ploceus cucullatus*), a passerine bird, indicate the generality of the code (N. Collias 1963).

The number of vocal signals or calls of birds has often been underestimated. Mrs. Nice (1943) described 21 "chief vocalizations" for the Song Sparrow, in the pre-spectrograph age. The Red Junglefowl has over 20 distinct and readily recognizable vocal signals, supported by spectrographic analysis (N. Collias 1987), as does the Village Weaver (Collias 1963 and unpubl. data). Not many birds have been observed sufficiently to yield such an extensive repertoire of vocal signals (Kroodsma and Miller 1996). In species with a graded and overlapping repertoire of vocal signals, quantitative analysis shows that different vocal signals can be readily recognized, for example in the Brown Noddy, *Anous stolidus* (Riska 1986).

DELTA WATERFOWL RESEARCH STATION (1953–1955). FILIAL IMPRINTING OF WILD DUCKLINGS

On recommendation by Mrs. Nice to the director, H. Albert Hochbaum, we were able to spend three summers at this research station at the south end of Lake Manitoba, Canada.

The station operated a large incubator in which eggs collected from nests of various waterbirds in the wild were hatched and made available to investigators. With Redhead (*Aythya americana*) ducklings, we confirmed that the day of hatching is a sensitive period for imprinting as Fabricius (1951) had found for other ducks. We also found that ducklings followed a substitute parent better and better as imprinting proceeded (Fig. 2); i.e., filial imprinting is self-reinforced and a form of learning defined as improvement of performance with practice (Collias and Collias 1956). This means the day of hatching in ducks, as in chickens, is a critical time during which mother and young gradually develop strong social bonds to each other.

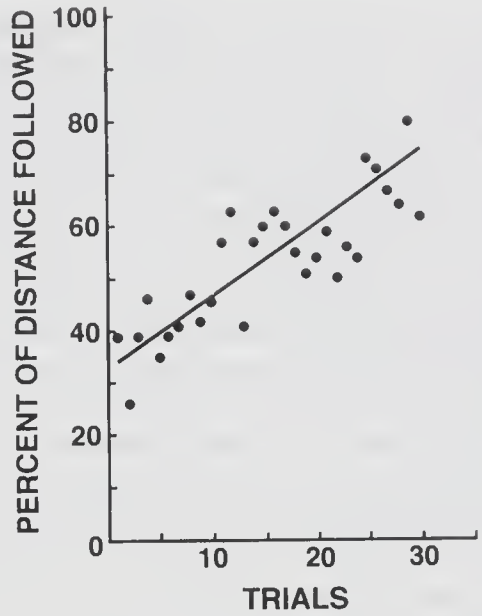

FIG. 2. Self-reinforcement of filial following. Redhead ducklings on day of hatching follow a person over standard course and distance better with each successive trial. Each dot is an average of 10 ducklings tested individually. (After Collias and Collias 1956).

Observations on two species of ducks in nature showed that the ducklings spend most or all of the day of hatching in the nest with the mother. Thus, after the first young hatched, a Blue-winged Teal (*Anas discors*) hen led her brood from the nest about 18 hours later, a Canvasback (*Aythya valisineria*) hen only after 24 hours in the nest (Collias and Collias 1956).

For her graduate research at Clark University, Mrs. Nice (1910) had counted various natural foods eaten by a very tame Northern Bobwhite (*Colinus virginianus*) that was imprinted on her. Similarly, at Delta we imprinted several species of wild ducklings to ourselves as substitute parents so that we could watch details of their feeding behavior as

closely as we wished without disturbing the ducklings in the least. Different species of ducklings placed together in the same white enamel pan, with various small aquatic invertebrates that we collected from the marsh, preferred to feed on different species of invertebrates. For example, a Blue-winged Teal duckling placed in the pan along with small snails and *Daphnia* ate the snails first, whereas a Ruddy Duck (*Oxyura jamaicensis*) duckling ignored the snails and strained out all the *Daphnia* (Collias and Collias 1963). In theory, such different feeding specializations illustrate the idea of the ecological niche and the principle of competitive exclusion, whereby different species of animals can live together in a community (Hutchinson 1978).

WEAVERBIRDS AND EVOLUTION OF NEST-BUILDING BEHAVIOR (From 1956)

At the end of her autobiography (1979), Mrs. Nice expressed a long cherished wish that she could have gone to the arctic and to the tropics. Modern travel facilities and greatly enhanced financial support for research have now made such things possible for many of us. The National Science Foundation was founded in 1950, and a few years later Elsie and I applied for a joint grant to go to Africa for a comparative study of nests and nesting behavior of weaverbirds. This was something that I had wanted to do ever since reading Alfred Emerson's (1938) classic monograph on termite nests as a study in the phylogeny of behavior. To our surprise, we received the grant and my dream was about to be realized.

Our friend, John Emlen, suggested we contact James Chapin of the American Museum of Natural History, who was then residing with his wife Ruth, in central Africa at a Belgian research station for tropical diseases. The Chapins were of inestimable help to us in many ways. The Belgians also helped us greatly. The director of the station even had a 12-m observation tower built for us next to a tree with a breeding colony of Village Weavers (*Ploceus cucullatus*). We caught many of these birds in mist nets and were able to make one of the first studies in Africa of birds color-banded as individuals (Collias and Collias 1959).

The male Village Weaver weaves the outer shell of the nest and with special displays and calls endeavors to attract an unmated female to enter his nest. If she accepts, she lines the nest with fine grass tops and often also with feathers, mates with the male, incubates, and does most or all of the work of feeding the nestlings. The male builds more nests and tries to attract more mates in this polygynous species. But if his nest is rejected repeatedly by females, the male tears it down and weaves a fresh nest in its place. He may have to build many nests for each one that fledges a brood. Each brood leaves with the female.

Evolution of weaving (Collias and Collias 1964, 1984).—Small body size and ability to construct a nest and place it in a wide range of nest sites may have been key factors in the origin and evolution of passerine birds (Order Passeriformes; N. Collias 1997). Like many other tropical passerine birds, weavers build roofed nests (Collias and Collias 1964, 1984; N. Collias 1997). In Africa, we traveled about to places Jim Chapin recommended, and we found as many nests of weavers as we could (Collias and Collias 1964). We found that only the Ploceinae (true weavers) of the seven subfamilies of Ploceidae (weavers) then recognized by Chapin (1954) truly weaves the nest, using interlocking loops of long green flexible strips torn from the leaves of grasses or palms. Sibley and Monroe (1990) unite four of Chapin's subfamilies into one that they call Ploceinae, but recognize much the same relationships. Weaving is a primary adaptation that enables safer placement of the nest which is suspended from twigs or vines near the periphery of trees, or the nest is slung between upright reed stems over water. The other subfamilies recognized by Chapin thatch their nests of stiff, often dry grass stems or sometimes light twigs.

Some of the true weavers add a long entrance tube about the bottom entrance of the nest that probably helps protect from snakes. There is a convergent evolution of entrance tubes in African and Asiatic species of weavers.

In the lowland rain forest of eastern Zaire, I collected the nest of *Malimbus cassini*, Cassin's Malimbe, also now known as the Black-throated Malimbe. This nest, with its very long, neatly woven entrance tube, is I think the most finely constructed nest of any bird in

the world. I knew of no specimen of this nest at that time in any American museum.

The genus *Euplectes* consists of true weavers which include a variety of bishop birds and widowbirds. They have elaborate flight displays but their nests illustrate regressive evolution of weaving (Craig 1980). In South Africa, we found a ground nest of the Long-tailed Widowbird (*E. progne*); this nest had only a very thin woven outer shell over a thick nonwoven lining of brown grasses.

Evolution of gregarious nesting by weavers.—Whereas forest-dwelling weavers are often solitary nesters, weavers of open country with an abundance of grass seeds and insects frequently nest in a colony, often in isolated trees (Chapin 1954, Crook 1962). Other things that favor gregarious nesting include feeding in large flocks well away from the nesting grounds, social guidance to good food sources, scarcity of trees for nests, and special protection from enemies by cooperative defense, or nesting in very thorny trees, or close to nests of stinging insects (reviewed by Collias and Collias 1984; see also Siegel-Causey and Khartonov 1990).

Social stimulation may also play a role in gregarious nesting. In Senegal, we found that colonies of Village Weavers with fewer than ten adult males attracted disproportionately and significantly fewer females than did males of larger colonies (Collias and Collias 1969). This is an example of the F. Fraser Darling (1938) principle of social stimulation to breeding. At UCLA, we found that moderate crowding of Village Weavers in large aviaries stimulated renewed breeding and extended the breeding season (Victoria and Collias 1973).

Gregarious nesting culminates in the famous apartment-style nest of the Sociable Weaver (*Philetairus socius*) of southwestern Africa (Collias and Collias 1964, 1978; Maclean 1973). The huge compound nest is thatched of straws with light twigs added to the communally built roof that helps protect the birds from some enemies, sun and weather. The underside of a nest mass has numerous openings to the separate nest chambers. A colony we saw in South Africa was said by local farmers to have occupied the same two trees for over 100 years. Our colleagues at UCLA, Bartholomew, White, and Howell (1976) found that the larger the nest mass, the greater the thermal homeostasis in the nest of this species (see also White et al. 1975).

The Sociable Weaver belongs to the subfamily Plocepasserinae (of Chapin 1954) as do the Grey-headed Social Weaver (*Pseudonigrita arnaudi*) and the White-browed Sparrow Weaver (*Plocepasseri mahali*), both of which we studied in Kenya (Collias and Collias 1978, 1980). The individual nests of the latter two species are often in physical contact, but lack a communal roof, and their sleeping nests have two entrance holes, an obvious defense against nocturnal predators. In contrast to the Sociable Weaver and the Grey-headed Social Weaver which may nest in large colonies and forage in large flocks well away from the nest trees, the White-browed Sparrow Weaver nests in small cooperatively breeding groups and defends a small group territory within which it feeds. The Plocepasserinae illustrate the Friedmann (1935) principle of colonial breeding in species of birds whose nesting and feeding grounds are spatially separated, whereas birds that feed in their reproductive area are generally solitary or less gregarious nesters.

Division of labor between male and female Village Weavers.—The division of labor between male and female birds in breeding behavior can be measured in terms of metabolic demands of the acts involved (Orians 1961; Collias and Collias 1967a, 1976; Paynter 1974). As a rough estimate of a very energy demanding act, flying by the Village Weaver takes about six times the energy as just resting under the same conditions. The male uses much flying energy for building nests that are unsuccessful. Putting the total amount of flying to gather nest materials into energy terms, we estimated for the central African race *P. c. nigriceps* that the male Village Weaver did 6–7 times as much work for nest building as did the female who merely lines the nest. By the same criterion of amount of flying required, the female did about twice as much work in foraging for food for the nestlings as did the male. Details of the analysis are given elsewhere (Collias and Collias 1967a, 1984:183–187).

The division of labor between male and female varies in different subspecies of Village Weaver (Table 1; Collias and Collias 1967a, 1970, 1971, 1984). In the west African race,

TABLE 1. Nests, polygyny, and nestling care in three races of Village Weaver, *Ploceus cucullatus*.[a]

	Western Africa *cucullatus*	Central Africa *nigriceps*	Southern Africa *spilonotus*
Aver. min. temp. when breeding	24° C	11° C	14° C
Number of males	9	18	11
Nests built in two weeks	3.3	1.4	1.9
Mates per male	3.1	1.8	2.0
Feeding rate per hour per nest:			
by male	0.1	2.3	1.4
by female	4.1	4.7	4.2
number of nests	15	11	39

[a] After Collias and Collias 1984:55.

the male scarcely feeds the nestlings and devotes his energy to building more nests and getting more mates, and he is more polygynous. The central African race was observed in a cool mountain habitat where the young apparently need more food, and the male often helped the female feed the nestlings, leaving him less time to build nests and get mates. The south African race is intermediate.

It is desirable to measure actual energy expenditure directly in the field. During the last two decades (Carey 1996), measurement of field metabolic rates has proved feasible with the doubly-labled water technique, clearly described by Nagy (1989). This technique measures CO_2 production rate and therefore overall energy expenditure over a specific period of time. For example, Flint and Nagy (1984) of UCLA found that the metabolic rate during flight of free-ranging Sooty Terns (*Sterna fuscata*) was about five times the standard resting metabolic rate.

Mate selection by the female Village Weaver.—Darwin's (1871) theory of sexual selection has attracted renewed attention in the last two decades (Andersson 1994), but Darwin had little to say about the role of nest-building behavior in courtship and mate selection. Long ago, Mrs. Nice (1943:179) pointed out that for birds "Symbolic building is characteristic of courtship in many species." The male Village Weaver carries this process one step further in that he weaves the complete outer shell of the nest that he then displays to unmated females.

Over the years we and our associates at UCLA did many controlled experiments on mate selection by the female Village Weaver in large outdoor aviaries. Doctoral and postdoctoral students on this problem have included Janice Victoria McClean, Catherine H. Jacobs, Florence McAlary McFarland and Cathleen R. Cox.

To attract an unmated female, each male of the colony hangs beneath the bottom entrance to his nest flapping his wings vigorously and uttering cries distinctive of each individual. It is a spectacular sight when all males of a colony display and call simultaneously. A visiting female inspects the nest interior and signifies her acceptance by lining the nest and copulating with the male.

Janice (Victoria 1969) found that both a male and his nest are essential for a female to choose a mate and lay eggs. Cathy (Jacobs et al. 1978) found that nests accepted by females were displayed by the male more than twice as often on the day of acceptance as nests that were rejected. The male's wing display reveals and is greatly enhanced by the bright yellow wing linings, and if we painted the wings black, such males attracted significantly fewer mates than did control males (E. Collias et al. 1979). Very young adult males and very old males are also discriminated against by the females (N. Collias et al. 1986). A female may change mates between broods, but she has a significant tendency to select her previous mate or a familiar territory for subsequent broods (McAlary 1985).

A nest has to last at least a month from the time the female accepts it until the young fledge. As a nest ages, it turns brown. The female prefers a fresh green nest, and she prefers a fresh nest painted green to a fresh nest painted brown (Jacobs et al. 1978), so color of the nest is one factor in her choice.

The strength of nest materials is very important to the female's choice. If a male's nest is repeatedly rejected, he tears it down and builds a fresh nest in its place, so fragmented materials from discarded old nests litter the ground. If the birds in an aviary are given no fresh nest materials, they will pick up and build nests of the old fragmented materials. A male displays his most recently built nest the most, and so may induce a female to temporarily accept such a trash nest. But we and our associates found that females laid eggs in significantly fewer trash nests than in still older

brown nests built of normal materials (Collias and Collias 1984).

In conclusion, the nest of the male Village Weaver, as well as the male himself, are both important considerations in the female's choice of a mate.

RED JUNGLEFOWL BEHAVIOR AND MECHANISMS OF EVOLUTION (From 1960)

Since my research career began with the analysis of behavior in domestic chickens, and, yet with a basic drive as a naturalist, it was understandable that I should be most curious as to the behavior in nature of the wild ancestor of the domestic fowl, i.e., the Red Junglefowl. During the academic year of 1962–1963, with financial support from the National Science Foundation and the Guggenheim Foundation, we were able to carry out a field study of this bird in nature (Collias and Collias 1967b), with special reference to its behavioral ecology and population breeding structure. We then tried to relate our results to mechanisms of evolution.

The principal theory relating genetics and evolution is the theory of Sewall Wright (1932, 1978a) that adaptative evolution depends most importantly on the shifting balance between the factors of evolution acting on a species that is subdivided into many partially isolated local populations. This theory is opposed to the idea that a species consists basically of a single randomly breeding population.

The significant question here is the nature of the breeding structure of populations in nature. One of the first attempts to relate the population structure of a wild bird species in nature to Wright's theory was in 1947 when Alden H. Miller plotted the population data of Mrs. Nice on the Song Sparrow to emphasize very limited dispersal distance of juvenile birds from their birthplace to breeding place. Miller (1947:139) concluded that the Song Sparrow, an abundant and widespread species, "actually is seen to exist in small effective breeding units" subject to considerable random differentiation in accord with Wright's theory. Wright (1940) considered especially important for evolution the case where local populations are liable to frequent extinction with restoration from a few stray immigrants, a phenomenon shown recently to occur frequently in color-banded populations of the Song Sparrow on small islands off the coast of British Columbia (Smith et al. 1996).

TABLE 2. Principles of animal breeding in evolution theory.[a]

Animal breeding	Evolution theory
1. Partially inbred lines	1. Random genetic drift in local populations
2. Mass selection	2. Selection between individuals and families
3. Cross breeding and line breeding	3. Differential emigration from local populations

[a] After Sewall Wright.

Wright (1978b) states that he derived his theory of the mechanisms of evolution from the principles and history of animal breeding (Table 2). Evidence from the breeding of chickens supports his theory (Collias and Collias 1996). Many new breeds and varieties of chickens have been produced by a combination of cross breeding and line breeding. As the primary and perhaps sole ancestor of the much studied domestic fowl, the Red Junglefowl is eminently suited for a study of genetic mechanisms in evolution.

After making a preliminary study of a free-ranging population of this species on the grounds of the San Diego Zoo, we visited southeast Asia, and then we went on to India for a study of the bird during its breeding season. Dr. Salim Ali of the Bombay Natural History Society advised us that a good place to find Red Junglefowl was in the Saharanpur forest district in the Himalayan foothills. There we received much help from the Wildlife Preservation Society of India. We observed the junglefowl from a platform in a tree, from a car, through a telescope when they came to drink at a waterhole, by following them about from elephant back, and by capturing them in nets and nooses with the assistance of the local people. The appearance of chicks coincided with onset of the rains and of flights of termites, an important food for the chicks, and this coincidence may help determine the breeding season.

We located roosts when the cocks crowed at dawn. The roosts were located in or near small branch ravines in western Thailand

(Collias and Saichuae 1967), and along larger water courses in India. When the birds were not disturbed they occupied the same roosts throughout the breeding season in India (Collias and Collias 1967b).

There seemed to be little difference between the behavior of Red Junglefowl in nature and in the free-living population at the San Diego Zoo where the birds formed separate populations in different ravines with very little interchange between local populations (Collias et al. 1966). We had color-banded most of the junglefowl in the zoo, and now focused on one large ravine where over a 7-year period we were able to get the lifetime breeding success of many of the birds, something that would have been very difficult in the field. We found that only a very small proportion of the birds, including the most dominant cock and most dominant hens, produced most of the adults of succeeding generations (Collias et al. 1994, Collias and Collias 1996). Of 8 successive males at the top of the peck order of cocks, one male (Male AA) had a longer tenure and copulated more often than the other 7 despots combined. He also mated twice as often as his 19 subordinates put together. The three hens at the top the peck order of hens added more offspring of breeding age to the population than did the remaining 25 adult hens of the flock for which we had lifetime breeding success. These findings accord with the dynasty principle elucidated by Newton (1989) in his summary of long-term studies by various investigators of different bird species in nature. When allowance was made for differential production of progeny and isolation by distance, the genetically effective breeding size of our Red Junglefowl population was estimated at only about 13% of the adult population (Collias and Collias 1996).

In conclusion, the behavior of the Red Junglefowl can be related to Wright's shifting balance theory of evolution through the effect of behavior on the breeding structure of populations. Social behavior exerts a reciprocal effect on evolution by structuring the population into traditional roosts and by greatly reducing the genetically effective breeding size of local populations through competition among individuals and families. Therefore, considerable random differentiation in and among local populations is expected, aside from local differences in conditions of selection. In a recent review of electrophoretic studies of allozyme variation in wild populations of 63 species of birds, Stangel (1991) found that island populations were significantly more differentiated than mainland populations, and that differences were significantly correlated with distance between sample localities.

The second part of this presentation of our research is given by Elsie, who describes some aspects of the development of behavior in birds, and also genetics of egg-color polymorphism as related to behavior.

I am honored to be asked along with my husband to give the first Margaret Morse Nice lecture. I grew up in northern Ohio during the period when Mrs. Nice did her classic field study of the Song Sparrow in Columbus, Ohio. However, I did not meet Mrs. Nice until after Nick and I were married.

As my husband mentioned we met at the University of Wisconsin where I was finishing my Ph.D. work. We were married the next year. Ever since we have worked as a team on the behavior of birds, in this country and overseas.

INHERITED AND LEARNED COLOR PREFERENCES

*Initial response to parental bill color by chicks of Franklin's Gull (*Larus pipixcan*).*—While at the Delta Waterfowl Research Station in 1955 we did an experiment on the initial response of incubator-hatched Franklin's Gull chicks to parental bill color (Collias and Collias 1957).

We presented two different bill colors simultaneously to a Franklin's Gull chick on the day it hatched in order to test the very first responses of the chick to parental bill color. The method used was to present to the chick a flat piece of immobile cardboard on which two simple models of adult Franklin's Gull heads were facing each other. Each head had a differently colored bill. The bills of the two heads were actually holes in the cardboard behind which different colors could be placed on both sides. The impression of motion was accomplished by having a light behind the heads flash on and off 85 times a minute,

stimulating the chicks to respond to the models. The chicks were taken right from the incubator and it was the first experience the chicks had with any color or the opportunity to peck at a bill or to even see a shape like that of an adult gull's head.

The colors tested were red, the color of an adult Franklin's Gull bill, versus white, or red versus green. The number of times a chick pecked at each color was recorded. Seventeen chicks each tested for six minutes, pecked the red bill 15 times more often than they pecked at the white bill and 4 times more often than they pecked at the green bill. Both results were statistically significant. We concluded that newly hatched Franklin's Gull chicks have a genetically determined predisposition to peck at a parental bill of the normal red color over white or green. We believe this experiment was the first confirmation with incubator-hatched young and without the use of hand-held models of the classic experiments by Tinbergen and Perdeck (1950) showing that the feeding responses of newly hatched Herring Gull (*Larus argentatus*) chicks are stimulated by the sight of the red spot on the lower mandible of the yellow bill of the parent.

*Anna's Hummingbirds (*Calypte anna*) trained to select different colors in feeding.*— Since most of the things one can buy for feeding hummingbirds are red, I decided to test if hummers really had a preference for red. I tested red, blue, yellow and colorless solutions of sugar water in various experiments (Collias and Collias 1968).

I trained hummers to come to a given color by presenting all four colors simultaneously, but only the solution to which the humming birds in our garden were being trained had sugar in it. All the other colors were just colored water.

When testing, I presented the same colors as in the training period but this time all colors were just water without sugar. In all cases the bird visited the color to which it had been trained by far the most often. This result showed a tendency to persist at a given color that indicates a good source of nectar before shifting to another color.

When I tested all four colors in different test tube feeders with the same concentration of sugar I found the hummers would start on one tube and finish that tube completely before they had finished half of any other color. This result shows a tendency to exploit a known source of nectar before exploring another regardless of color.

In conclusion, Anna's Hummingbirds can probably learn any flower color that indicates a good nectar flow.

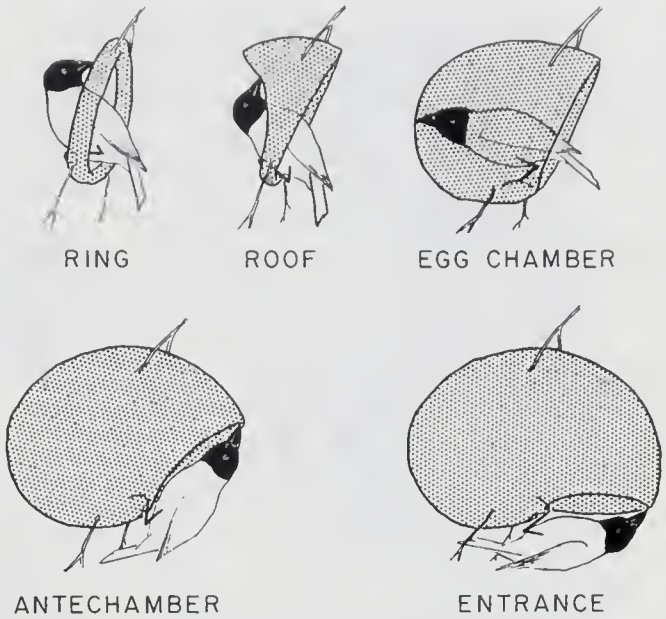

FIG. 3. Sequence of stages followed by a male Village Weaver in weaving his nest (Collias and Collias 1962).

WEAVING OF THE NEST BY THE MALE VILLAGE WEAVER

As you know we studied weaverbirds, particularly the Village Weaver for many years, and I am going to describe some phases of our work. First, I want to describe how a weaverbird makes a nest (Collias and Collias 1962, 1984).

A typical Village Weaverbird nest built by an experienced male adult weaver doesn't look much like a typical nest from North America. It is roofed, has a bottom entrance, and is woven of strips torn from the leaves of grasses or palms.

Figure 3 shows the various stages in building of a Village Weaverbird nest. Each stage of the nest provides the stimulus for the next stage.

(1) Only the male weaves a nest and he selects a site which is quite far out on a small branch, and preferably at a fork. He first builds a ring. Then while standing in the ring he builds the rest of the nest. He

always stands in the same place and always faces in the same direction.

(2) He builds the roof over his head and in front of him pushing and building out as far as he can, and so ends up building the globular nest chamber.

(3) Then he builds over his head toward his back and forms the antechamber. When he gets the antechamber down to the horizontal he neatly finishes off the entrance. Then he thatches a ceiling of relatively short wide strips.

(4) His standing in one place and pushing out in all directions determines the size and shape of the nest.

(5) The threshold where he keeps his feet serves as a ridge to keep the eggs from rolling out of the bottom of the nest chamber.

(6) After a female accepts a nest he adds a short entrance tube 4–8 cm long. This is the only part of the nest he adds while outside the nest, probably because the female won't let the male enter the nest after she accepts it.

Figure 4 shows some of the motions a male goes through to push and pull a strip into his ring. Note that if the strip is too long for him to push all of it through, he brings the loop around and weaves it in. He then takes the loose end of the strip and weaves it in.

After studying how a weaver makes his nest we attempted to weave a nest ourselves with forceps, using as near as possible the same general techniques as the male, and we managed to make a nest that was a reasonable facsimile of a normal nest (illustrated in Collias and Collias 1962).

DEVELOPMENT OF NEST BUILDING BY THE MALE VILLAGE WEAVER (Collias and Collias 1964, 1973)

Reports in the literature indicate that a bird which was denied access to nest materials until it was an adult built a first nest that was just like that of an experienced bird. This is not true of the Village Weaverbird as we saw in Africa. Males do not get adult plumage until their second year, and we saw colonies of yearling males gathered in a tree practicing building nests. The nest of a young weaverbird doesn't look much like the nest of the adult (Collias and Collias 1964). So we decided to see what a bird had to develop or learn in order to build a typical nest.

A young Village Weaver that I raised from before he had his eyes open we called Tex as a shortened form of *Textor* which means weaver and which at that time was the generic name of this group of weaverbirds. Little did I realize at the time that Tex was only the first of 41 weaverbirds I was going to hand rear.

After Tex could feed himself we kept him in a cage that was large enough that we could furnish him with giant reed grass (*Arundo donax*) for nest materials, as we did the adults in the outdoor aviary. A nest built by Tex in his second year was pretty good. At this point he had neither seen nor even heard another Village Weaver so neither tuition nor example is necessary for a male weaver to build a nest—then just what was necessary?

I reared some male weavers in the complete absence of any natural materials that could be used for building. When these birds were seven months old I tested their preference for different colors with colored toothpicks which gave a standard size, shape and weight, representing nest materials. During the first four days of testing, preference of the young weavers for green increased significantly (P = 0.01) from 38% to 71%.

At first the males will try to weave with any strip even if it is much too short. By measuring the length of all the strips in two nests of the same bird, we found that a male Village Weaver in his first breeding season as an adult builds with strips that average twice as long as those he used as a yearling.

The birds also have to learn the mechanics of weaving and where to weave. We found retarded development of weaving ability in young male Village Weavers that had been completely deprived of normal nest material until almost one year of age. As yearlings, the controls not only tore more strips, they wove a significantly bigger percentage of their strips (Collias and Collias 1973). However, both groups wove by far the majority of strips on the wire of the cage—an easier place to weave than on the twigs. In fact the deprived yearlings didn't weave anything on the twigs.

The next year, after considerable practice, the percentage of total strips woven by deprived and nondeprived birds was not signif-

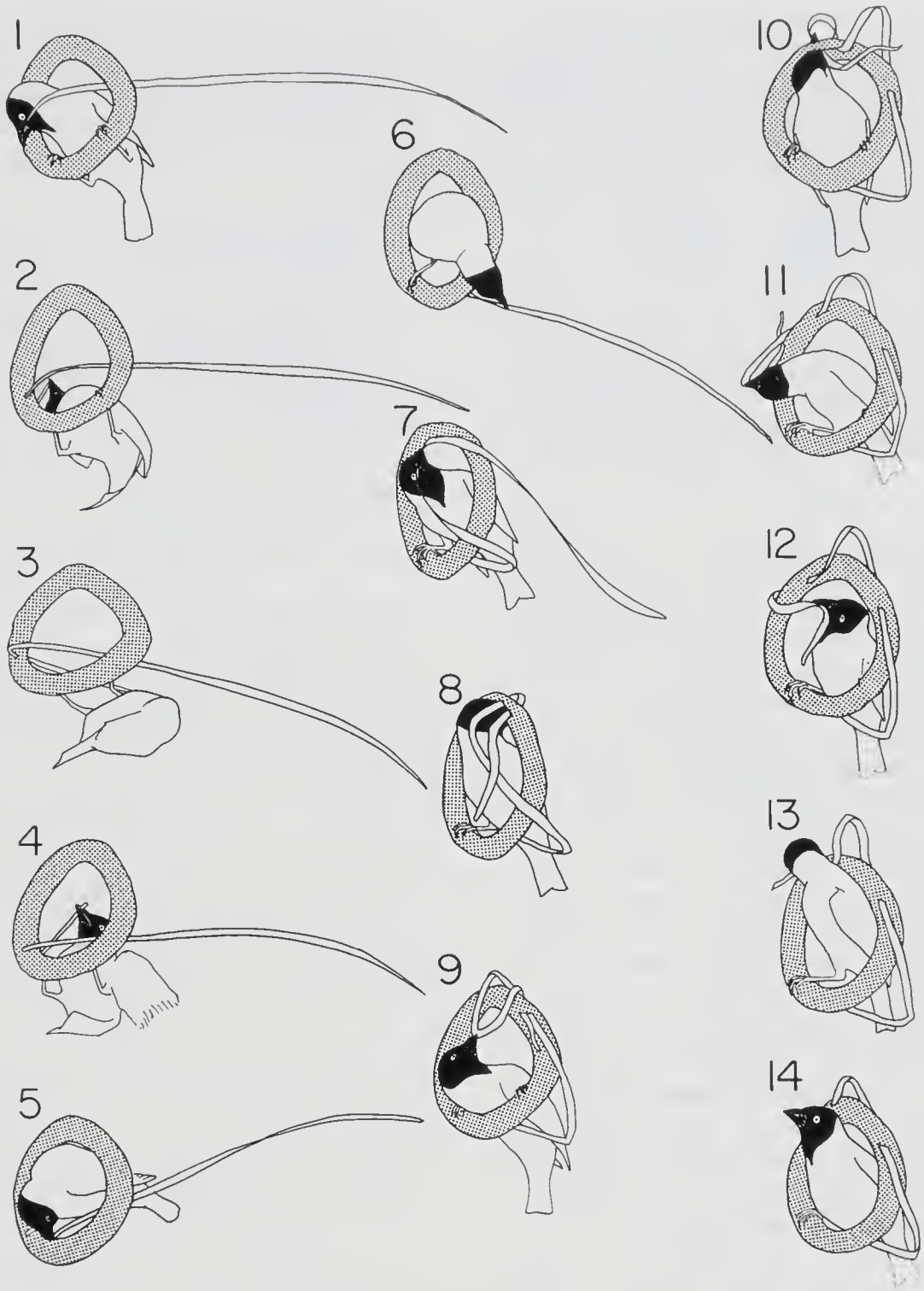

FIG. 4. Typical sequence of movements by a male Village Weaver as he weaves a single strip of grass or palm leaf into his ring (Collias and Collias 1962). Drawn by Nicholas Collias from motion picture frames.

icantly different. However, the number of strips woven on twigs was significantly different (Collias and Collias 1973).

When watching young Village Weavers learning to weave we have often seen a subordinate tear a strip and immediately have it taken away from him by a more dominant bird. The dominant bird often then used this strip to weave. Of course this means that the dominant bird has much more opportunity to practice weaving. Since the young weavers need practice in order to perfect the skills used in weaving the dominant birds actually perfected their weaving skills and often went on to build a nest at a much earlier age than did the subordinate birds.

When matched with control birds that had a similar dominance level, the deprived young

wove a significantly smaller percentage of their strips (Collias and Collias 1973). The deprived birds in this case were only partially deprived in that they had access to nest material until they were seven weeks old and then were not given any nest material until the age of about one year when this test was done.

A long-term example of the effect of lack of practice on subsequent ability to build a nest was Male LL who was at the bottom of the peck order in his group which had been completely deprived of nest materials after seven weeks of age. He would tear a strip only to have it promptly taken away by one of his cage mates. As a result Male LL had almost no chance to practice weaving, and never learned to build a nest. He lived seven years, and spent several breeding seasons in a large outdoor aviary with a number of the other weavers. He changed to full breeding plumage each breeding season and held a territory, yet in all that time he never managed to build a nest. He would tear a strip and taking it to a perch spend hours playing with it but he never wove one strip. Thus weavers must have sufficient opportunity to weave when they are young or they never learn to weave.

Our colleague Cathy Jacobs who helped us a great deal in our studies on weaverbirds hand-reared a male Village Weaver she called Phineas. Cathy kept Phineas in her office for four years in a cage. Starting at about six months she supplied Phineas with many long strips she tore from palm fronds, at least once a week for a year and occasionally after that. He often wove his strips on the wire cage and wove a complete ring his second year. At four years he was put out in the large outdoor aviary. This aviary was supplied with a fresh palm frond daily for all the weavers. Phineas was unable to tear a single strip by himself although he did weave a crude nest from strips he took from other weavers. This shows that not only rather complicated weaving requires practice but also the more simple task of tearing a strip.

We induced an adult male weaver (RR) to build an abnormally long entrance tube on his nest by adding dangling strips with one end fastened to the entrance of his nest. Thereafter although he usually built a normal length tube he sometimes built a long one several times the normal length. None of these later nests were built with any help or incentive from us so he had learned to build a very long entrance tube after he became an adult.

In conclusion, our experiments on development of nest building by the Village Weaver showed:

(1) Self-reinforcement of inherited acts with experience.
(2) Building a species-specific nest requires practice but not a tutor.
(3) A young bird has a long sensitive period (months) for nest building.
(4) Adults can learn new building habits.

INHERITANCE OF EGG-COLOR POLYMORPHISM IN THE VILLAGE WEAVER

Now I am going to shift from the building of a nest to egg-color polymorphism in the Village Weaver. It seems a bit far from behavior but as Ernst Mayr (1958) has pointed out, behavior often precedes related morphological evolution.

Most birds in North America lay only one color of egg, but that is not true of the Village Weaver, the eggs of which vary widely in both color and spotting. The four background colors found in the Village Weaverbird are white, turquoise, emerald turquoise, and emerald. Each female lays the same type of eggs over her lifetime (E. Collias 1984).

For fourteen years we did experiments that required the female to make a choice between the nests built by the males. To maximize the number of choices that females made we removed the eggs of a clutch one or two days after the last egg was laid. Each egg was identified as to the female who laid it, the date laid and the male to whom the female was mated at that time.

By this method we accumulated well over a thousand eggs. Suddenly one day I realized that now I had an opportunity to explore the genetics of egg color in a passerine bird (E. Collias 1993), something that had never been done before, for in addition to having the eggs, we had been breeding these birds for years and knew the parents and sibs of all our birds except, of course, our original flock. I identified the color of each egg from the Villalobos Color Atlas which divides the spectrum into 33 hues and then subdivides and

grades them by chromaticity (the amount of attenuation of the hue) and lightness (from black to white).

For example, examination of variation in 59 eggs laid by female ABA over nine years showed that all her eggs were of turquoise hue, most were fairly light in color (Grade 17), intermediate in chromaticity (Grade 6), and all were unspotted.

From 20 different crosses between 13 males and 15 females which resulted in at least one daughter from whom we also obtained eggs, I postulated five hypotheses as to the inheritance of egg color: two, three, or four alleles at one locus, or two pairs of sex-linked alleles, or two pairs of autosomal alleles at two loci. On checking each hypothesis against the data I ruled out the first four.

Since space is limited, I will summarize the hypothesis that appears to explain the inheritance of egg color and recommend that for more details on the crosses, how I tested the hypotheses, and my reasoning with regard to acceptance or rejection, one can check my 1993 paper in The Auk.

The last hypothesis for the inheritance of egg color is two pairs of autosomal alleles at two loci and postulates the following:

Emerald—at least one dominant gene for emerald (E-), and only recessive genes for turquoise (tt).

Turquoise—at least one dominant gene for turquoise (T-), and only recessive genes for emerald (ee).

Emerald turquoise—at least one dominant gene for both emerald and turquoise (E-T-).

White—only recessive genes at both loci (ee, tt).

This hypothesis worked in all 20 crosses. The other four hypotheses fail to explain the data.

I shall give an example of how Hypothesis 5 worked—two pairs of autosomal alleles at two loci (Figure 5):

Male 1 (Ee, Tt)—mated with Female 1 who laid emerald turquoise (Ee, Tt) eggs. They had a daughter who laid white (ee, tt) eggs.

Male 1 (Ee, Tt)—also mated with Female 2 who laid white (ee, tt) eggs. They had two daughters one of whom laid turquoise (ee, Tt) eggs, the other laid emerald turquoise eggs (Ee, Tt).

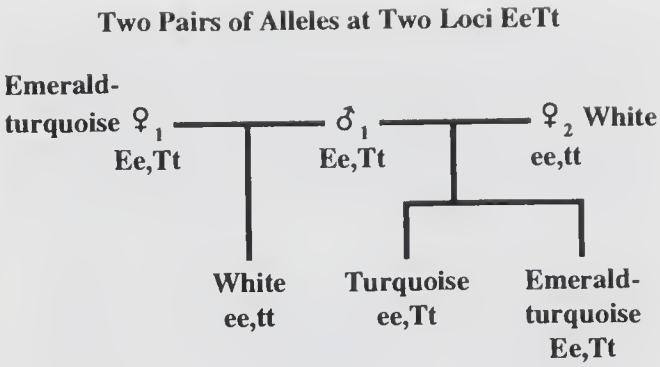

FIG. 5. Example of matings by Village Weavers and colors of eggs laid, consistent with hypothesis of a pair of alleles at each of two autosomal loci, with turquoise allele and emerald allele dominant over white allele but not over each other (emerald-turquoise egg; E. C. Collias 1993).

Therefore, these results are consistent with a hypothesis of two pairs of autosomal alleles at two loci for the inheritance of egg-color polymorphism in the Village Weaver.

Now why do Village Weavers have so many different kinds of eggs? Our colleague, Janice McLean, answered that question. She put other weaverbird eggs into a nest already containing eggs. Unless the added egg very closely resembled that of the host the strange eggs were immediately tossed out regardless of whether the added egg was the odd one in the clutch or if the female's own egg was the odd one (Victoria 1972).

This egg variability probably arose as a defense against nest parasitism. Did this develop as a defense against intraspecific or interspecific parasitism? I do not rule out either completely. However, I do not think intraspecific parasitism played a big part in the Village Weaver. We never saw any evidence of this type of egg parasitism in three breeding seasons in Africa. However, it does occur. Janice, in four years of observation in our aviaries saw two cases both under rather unusual circumstances. In one case where the eggs differed, the strange egg was ejected. In the other case in which both females had very similar eggs, the parasitic egg was accepted.

I think interspecific parasitism probably played an important role because of the work of Cruz and Wiley (1989) on the Village Weavers which were introduced into Hispaniola by the early 18th century. These weavers

were without brood parasites until the 1970s when the Shiny Cowbird (*Molothrus bonariensis*) arrived and laid in the weaver nests. The weavers did not reject the cowbird eggs although these were quite different from the weaver eggs. Evidently weavers had lost the egg rejection behavior in the intervening 200 yrs, which they certainly would not have done if intraspecific nest parasitism was common.

To summarize egg-color polymorphism in the Village Weaver:

(1) Each female weaver lays eggs with the same color characteristics all her life.
(2) The inheritance of background color of eggs is consistent with a hypothesis of 2 autosomal alleles at 2 different loci.
(3) A female will throw out any egg that differs markedly from her own eggs, a protection from brood parasitism.
(4) This favors selection for uniformity of eggs of the same female and variability between females.

Our research on bird behavior has given us much enjoyment and intellectual satisfaction over the years, as has the consequent interaction with many friendly and helpful students of birds. Foremost among the latter has been Margaret Morse Nice and the inspiration and guidance given by her research on the life of birds in nature.

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AVIAN COMMUNITIES IN BAYHEADS, WILLOWHEADS, AND SAWGRASS MARSHES OF THE CENTRAL EVERGLADES

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ABSTRACT.—We compared avian community composition, species richness, and total bird abundance among three vegetation types (bayheads, willowheads and marshes), and between a reduced-hydroperiod and relatively unimpacted landscape in the central Everglades during July–August, 1996. Our results showed that the collective Everglades bird community contained a substantial number of forest birds as well as marsh species. Red-winged Blackbirds (*Agelaius phoeniceus*), Common Yellowthroats (*Geothlypis trichas*), and White-eyed Vireos (*Vireo griseus*) accounted for 65% of total individual birds during the period of study. Wading birds accounted for a relatively small proportion of the total avian community. White-eyed Vireo was the most abundant bird species in bayheads and was closely associated with that habitat. Red-winged Blackbird and Common Yellowthroat were the most abundant species in both willowheads and marsh vegetation. We found no significant difference in bird abundance among vegetation types ($P > 0.05$) nor between landscapes ($P > 0.05$). We also found no difference in species richness between landscapes ($P > 0.05$). A significant ($P = 0.02$) interaction between vegetation and landscape indicated that species richness differed among vegetation types in the unimpacted landscape, but not in the reduced-hydroperiod landscape. In the unimpacted landscape we detected significantly more species in bayheads than the other two vegetation types (both tests, $P \leq 0.004$). An ordination revealed that in the unimpacted landscape, bird communities were more specific to vegetation types than in the reduced-hydroperiod landscape. Our study demonstrates that two characteristics of a relatively unimpacted landscape in the central Everglades are higher avian species richness and a more distinct avian community in bayheads than in willowheads or marshes. The Everglades restoration process will promote the conservation of avian diversity by restoring the landscape matrix of both marsh and bayhead vegetation. *Received 8 May 1997, accepted 3 Oct. 1997.*

The Everglades has been described as a vast lake covered with tall sawgrass (*Cladium jamaicense*) and studded with thousands of tree islands (Smith 1848 *in* Gunderson and Loftus 1993). The vertical structure of tree islands provides nesting and foraging opportunities for many avian species that could not otherwise exist in this marsh dominated ecosystem. Thus, the mosaic of naturally fragmented forest patches imbedded in expansive herbaceous marshes produces a landscape that supports both forest and marsh birds. The recent focus on the Everglades restoration effort (e.g., Cohn 1994, Ogden 1994, Culotta 1995) provides several examples of how birds are used to reflect the condition of an ecosystem. Despite the usefulness of birds as environmental indicators, habitat-specific associations of avian species inhabiting the Everglades are largely unknown. Only limited quantitative data exist on bird use of marshes (Kushlan and Kushlan 1977) and to the best of our knowledge, only qualitative data exist for tree islands (Robertson 1955, Robertson and Kushlan 1984, Richter and Meyers 1993).

In the Everglades, the term tree island has been used interchangeably to represent bayheads, cypressheads, willowheads, and hardwood hammocks. Bayheads are dominated by red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*), dahoon holly (*Ilex cassine*), and wax myrtle (*Myrica cerifera*) (Robertson 1955, Olmstead and Loope 1984, Gunderson 1994). Willowheads usually occur as monotypic stands of willow (*Salix caroliniana*; Loveless 1959, Gunderson and Loftus 1993) that are associated with soil disturbance (Gunderson 1994). Historical records of Everglades vegetation suggest that bayheads in the central Everglades have declined in number since the Central and Southern Florida Drainage Project was initiated in the 1910s (Davis et al. 1989), whereas willowheads have become much more widespread (Craighead 1971). The construction of impoundments to create the Water Conservation Areas (WCAs) has intensified these changes. Marshes with shorter hydroperiods (defined as the length of time an area is inundated with water) were created in northern portions of the reservoirs, as were

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marshes with longer hydroperiods and deeper water in southern regions of the reservoirs (Zaffke 1983). Tree island vegetation changed under both extremes with bayheads converting to willow and Brazilian pepper (*Schinus terebinthifolius*) in reduced hydroperiod areas and converting to willow, cattail (*Typha* spp.) and melaleuca (*Melaleuca quinquenervia*) in extended hydroperiod areas (Davis et al. 1989, Davis et al. 1994).

Creation of the impoundments also changed the landscape matrix of tree islands and marshes. In the reduced hydroperiod marshes of WCA-3A (i.e., the area north of I-75; Fig. 1), shrubs invaded the most severely drained portions and the aerial extent of cattail increased. Severe peat fires burned off muck edges of tree islands, thereby lowering the elevation and producing a vegetation shift away from the dense sawgrass fringe often associated with tree island edges (Zaffke 1983, Gunderson and Snyder 1994). Collectively, these changes produced a landscape of sawgrass marshes with scattered shrubs, cattail patches and smaller tree islands. The smaller tree islands have sharply defined edges that lack the extensive sawgrass fringe associated with tree islands in longer-hydroperiod marshes further south in WCA-3A.

The relationship between vegetation structure and bird density and diversity has been well-documented but was not always consistent among regions or studies (MacArthur and MacArthur 1961, Karr and Roth 1971, James and Wamer 1982, Mills et al. 1991, Willson and Comet 1996). Inconsistencies usually resulted from a specific measure of bird diversity or abundance not correlating as strongly with a particular measure of vegetation diversity or volume in one study as in another. Nevertheless, the generalization emerges that vertical vegetation structure and volume are often correlated with increased bird abundance and, or, diversity. Thus, we hypothesized that the greatest bird abundance and diversity would be in bayheads, willowheads, and marshes, respectively because of their vegetation structure. Vegetation changes that have occurred in the Everglades, such as increases in the number of monotypic willowheads and losses of bayheads, therefore, may have greatly altered the avian community.

Landscape patterns of vegetation in addition to the structure of individual tree islands, can also affect bird species diversity and density (Virkkala 1991, Steele 1992, Pearson 1993). The configuration of vegetation patches in the landscape affects the movements of organisms among patches, which has consequences for finding mates, avoiding predation, and finding adequate food resources. Thus, it is possible that bird communities associated with similar vegetation types may differ between landscapes with different patch configurations. The two contrasting landscapes in our study, likely caused by historic differences in water management, provided an opportunity to test these potential effects on the Everglades' bird community.

The ongoing Everglades restoration process has the potential to once again alter the mosaic of vegetation communities in the Everglades through a reduction in nutrient loads entering the WCAs and the establishment of more natural hydropatterns (South Florida Water Management District 1995). Hydropattern restoration will likely result in longer hydroperiods in northwestern WCA-3A and shorter hydroperiods in southeastern WCA-3A. Habitat associations of avian species will provide resource managers with critical information to predict the effects of landscape changes on the Everglades' bird community. We define community as a group of individuals of several species that co-occur in time and space (Wiens 1989a).

In this study, we compared bird communities among three vegetation types (bayheads, willowheads, and marshes), in both a reduced-hydroperiod and relatively unimpacted landscape in the central Everglades. Although the entire Everglades ecosystem has been affected by human activities to some degree, we use the term "unimpacted landscape" because the west-central portion of WCA-3A (Fig. 1) still has vegetative and hydrologic characteristics similar to those in historic accounts (Davis et al. 1994). We term the reduced-hydroperiod area in WCA-3A north of I-75 as "impacted." We addressed the management questions: (1) do bird communities differ among vegetation types, and (2) are bird communities within vegetation types similar in landscapes with different management histories?

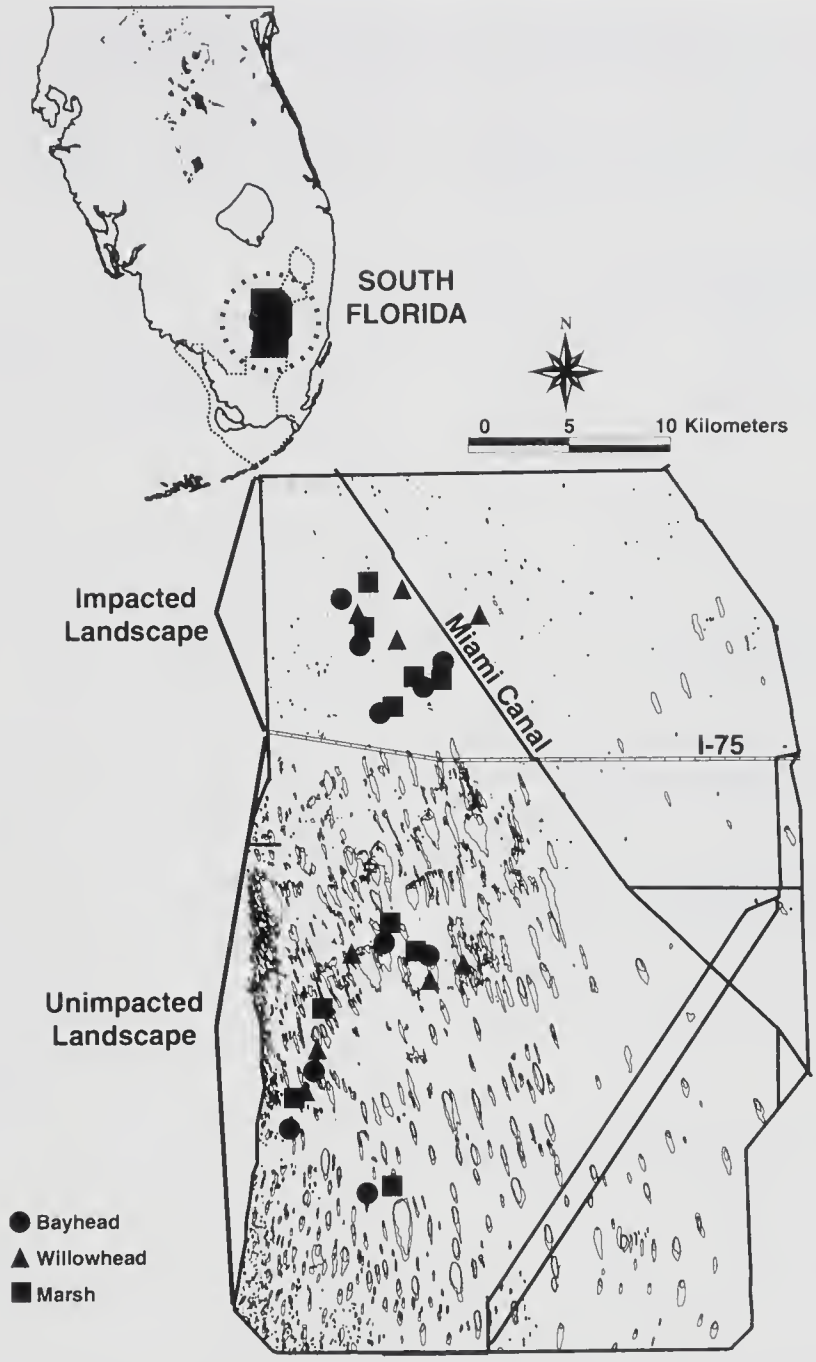

FIG. 1. Sampling sites in Water Conservation Area 3A in the central Everglades.

METHODS

Study area.—All study sites were located in WCA-3A (Fig. 1) within the central Everglades. We selected 14 sites (5 bayheads, 4 willowheads, and 5 marsh) in the impacted landscape and 15 sites (5 bayheads, 5 willowheads, and 5 marsh) south of I-75 in the unimpacted landscape. We assumed bayheads would be limited in number in the impacted landscape so we chose those sites first with the criteria that they contained more than 50% woody species other than willow, were qualitatively as similar as possible in composition and size, and were separated by at least 1 km. A distance of 1 km is greater than the territory size of most passerines and reduced the chance of counting the same individuals at more than one site. For the Ciconiiformes, this assumption probably does not hold true because of their tendency for long-range flights (Kushlan 1976). However, we surveyed adjacent sites in sequence and surveyed all sites within the same landscape in the same day to reduce the chances of individuals moving among sites. Willowheads were selected on the criteria of being the closest tree island of predominantly (>75%) willow, at least 1 km from other sites, and being as similar in size as possible based on availability. Only four willowheads met those criteria in the impacted landscape. Excluding one large bayhead, tree islands were small, averaging 5 ha. Island size did not differ significantly between landscapes ($P > 0.05$) nor among vegetation types ($P > 0.05$). The criteria for marsh sites were that they were at least 1 km from other sites and, for logistic reasons, close to the line of travel among tree islands.

Data collection.—Each site was surveyed by the same observer once per week for 4 weeks in July–August 1996 (17 Jul, 23 Jul, 30 Jul, 5 Aug). Surveys began within 30 minutes before or after sunrise and were usually completed by late morning. To reduce any variation in detection caused by time of day, we reversed the sequence in which sites were surveyed within landscapes each week. Because of the prolonged nesting season for many birds in south Florida (March–August), the intensity of singing by territorial males, and thus their detection probability, varied throughout the summer. Also, juveniles were present for much of the year. Therefore, we considered our surveys to be measures of relative abundance rather than absolute density of nesting pairs.

Surveys were conducted using a modified variable circular-plot method (Reynolds et al. 1980). Because of accessibility constraints, and to reduce disturbance to birds, plots at tree islands were centered on tree island edges. This protocol produced two semicircular subplots that consisted of either tree island or marsh vegetation. We believe that centering plots on island edges did not bias our counts toward "edge-species" because islands were too small to provide a true forest interior at the scale of individual bird territories. We recorded birds separately for each subplot and included during the analysis only those birds in the tree islands. To standardize our plot size and shape for marsh sites, we randomly selected the orientation of two semicircular subplots at each marsh site. Subplots remained fixed throughout the study. For the analysis of marsh sites, we included counts from only one randomly selected subplot.

We arrived at each site by airboat and preceded each survey with a two-minute waiting period to allow birds to adjust to initial disturbance. We then surveyed birds for the subsequent six minutes. We developed our methodology for this unique environment based on a pilot study which indicated that two minutes was sufficient to allow birds to recover from initial disturbance. Our pilot study also showed that six-minute surveys identified the majority of species at each plot and counts of up to 25 minutes produced little overall gain in species richness (e.g., Gates 1995).

During surveys, each bird seen or heard was identified to species when possible, and its distance from the survey point was estimated as <50 m, 50–100 m, and >100 m. We also recorded the subplot in which it occurred. Our pilot study indicated that the probability of detecting birds as a function of distance from observer decreased substantially beyond 100 m. Therefore during the analysis we excluded birds detected at more than 100 m. We also excluded birds that flew over the site without landing and may not have been associated with vegetation at our sampling sites.

In five instances we detected unidentified small passerines in the vegetation. These birds were classified as unknowns and were included in the analysis of total bird abundance but not of species richness patterns or multivariate analyses. During the final sampling period of our study we recorded the presence of Tree Swallows (*Tachycineta bicolor*). We believe these birds were migrants because of their initial appearance late in the season and because Tree Swallows are not known to nest in south Florida (Stevenson and Anderson 1994). To avoid confounding patterns of resident birds, we reported the presence of Tree Swallows in Table 1 but did not include them in any statistical analyses.

Univariate analyses.—We used a three-factor repeated measures design analyzed as a split-plot ANOVA with landscape and vegetation type as the crossed factors and sampling period as a repeated measure factor (Cody and Smith 1991). Dependent variables were species richness (i.e., the number of species/site/survey) and total bird abundance (i.e., the total individuals/site/survey). Statistical comparisons were made using PROC GLM in SAS (SAS Institute Inc. 1988) for a UNIX operating system. Differences in least-square means were considered significant at $P \leq 0.05$. Least significant difference tests were conducted on the least-square means when a model term was deemed significant as per our a priori critical level. We specified "site nested within landscape × vegetation" as the error term for least significant difference tests of landscape, vegetation, and landscape × vegetation.

Multivariate analyses.—To identify individual species patterns related to landscape and vegetation types without conducting an undesirably large number of univariate tests, we conducted a canonical variate analysis (CVA), also called canonical discriminant analysis, using PROC DISCRIM in SAS (SAS Institute Inc. 1988) for a UNIX operating system. This technique is an exploratory ordination procedure that reduces the dimensionality of the data by deriving linear combinations of the original variables (e.g., bird abundances) called canonical variates (CAN) (Williams 1983). Canonical variates are uncorrelated and constructed to maximize differences among groups defined by a single nominal variable. The effectiveness of a CAN in differentiating among groups can be evaluated with the canonical correlation coefficient, a measure of association between a canonical variate and the groups. This coefficient ranges from zero to one with large values indicating a strong relationship and zero indicating no relationship (Klecka 1980).

Canonical variate analysis differs from related ordination procedures, such as principal components analysis, in that principal components analysis maximizes total variance along the first ordination axis whereas CVA maximizes the ratio of the between-group sum of squares and the within-group sum of squares (ter Braak 1995). Thus, by examining the total structure coefficient, which is the pairwise correlation between a CAN and an original variable, it is possible to identify which of the original variables contribute most to differences among groups. In our study, the groups were vegetation types and the original variables were species abundance values at each site during each survey.

Because our initial univariate analyses indicated that the relationship between the avian community and

TABLE 1. Abundance and species richness of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.[a]

	Unimpacted landscape						Impacted landscape						All sites	
	Bayhead (n = 5)		Willowhead (n = 5)		Marsh (n = 5)		Bayhead (n = 5)		Willowhead (n = 4)		Marsh (n = 5)		(n = 29)	
Species	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Anhinga											0.05	0.11	0.01	0.05
Great Egret											0.05	0.11	0.01	0.05
Green Heron	0.05	0.11							0.13	0.14			0.03	0.08
Turkey Vulture	0.25	0.35	0.05	0.11	0.10	0.22	0.05	0.11	0.19	0.24	0.15	0.34	0.13	0.24
Osprey			0.05	0.11					0.06	0.13			0.02	0.06
Snail Kite					0.05	0.11							0.01	0.05
Red-shouldered Hawk	0.15	0.34											0.03	0.14
Common Moorhen			0.05	0.11	0.65	0.80	0.05	0.11	0.25	0.35	0.55	0.69	0.26	0.50
Yellow-billed Cuckoo							0.05	0.11	0.06	0.13			0.02	0.06
Great Horned Owl					0.05	0.11							0.01	0.05
Red-bellied Woodpecker	0.45	0.51	0.05	0.11			0.15	0.14	0.06	0.13			0.12	0.26
Eastern Kingbird	0.15	0.22					0.75	1.16					0.16	0.53
Tree Swallow					0.05	0.11					0.20	0.33	0.04	0.15
Carolina Wren	0.05	0.11											0.01	0.05
Blue-gray Gnatcatcher			0.05	0.11			0.10	0.22					0.03	0.10
Loggerhead Shrike							0.25	0.43			0.05	0.11	0.05	0.19
White-eyed Vireo	1.70	0.69	0.20	0.27			1.10	0.78	0.88	0.97			0.64	0.83
Common Yellowthroat	0.50	0.35	0.95	0.94	0.80	0.60	0.35	0.22	0.56	0.13	0.65	0.34	0.64	0.51
Northern Cardinal	0.70	0.51	0.20	0.21			0.10	0.14	0.25	0.29			0.21	0.34
Red-winged Blackbird	0.55	0.21	1.40	0.63	1.10	0.68	0.95	0.69	2.31	1.09	2.65	1.13	1.47	1.04
Boat-tailed Grackle	0.85	0.58	0.30	0.33			0.40	0.38	0.13	0.14	0.30	0.11	0.34	0.40
Unknown[b]	0.20	0.21	0.05	0.11			0.05	0.11					0.05	0.12
All species	5.60	1.88	3.35	0.72	2.80	1.12	4.35	1.72	4.88	1.64	4.65	1.59	4.25	1.66
Species richness	3.35	0.95	1.95	0.45	1.60	0.45	2.35	0.84	2.81	0.88	2.10	0.45	2.34	0.86

[a] Values represent the average number of individuals or species detected at a site during a 6-min survey.
[b] Unidentified small passerines.

vegetation types differed between landscapes, we conducted separate CVAs for each landscape. We excluded from the analyses four species for each landscape that were detected during only one survey and thus had no variance. Species excluded from the analysis in the unimpacted landscape were Anhinga (*Anhinga anhinga*), Great Egret (*Casmerodius albus*), Loggerhead Shrike (*Lanius ludovicianus*), and Yellow-billed Cuckoo (*Coccyzus americanus*). Species excluded from the analyses in the impacted landscape were Carolina Wren (*Thryothorus ludovicianus*), Great Horned Owl (*Bubo virginianus*), Red-shouldered Hawk (*Buteo lineatus*), and Snail Kite (*Rostrhamus sociabilis*).

RESULTS

Community composition.—With all sites pooled, the three most abundant species were Red-winged Blackbird (*Agelaius phoeniceus*), Common Yellowthroat (*Geothlypis trichas*), and White-eyed Vireo (*Vireo griseus*). Collectively they accounted for 65% of all individuals.

In the unimpacted landscape, the most abundant species in bayheads were White-eyed Vireo, Boat-tailed Grackle (*Quiscalus major*), Northern Cardinal (*Cardinalis cardinalis*), Red-winged Blackbird, Common Yellowthroat, and Red-bellied Woodpecker (*Melanerpes carolinus*), respectively (Table 1). Willowhead communities were dominated by Red-winged Blackbird and Common Yellowthroat, respectively. Marsh communities were dominated by Red-winged Blackbird, Common Yellowthroat and Common Moorhen (*Gallinula chloropus*), respectively.

The CVA of bird communities in the unimpacted landscape indicated that the discriminatory power of CAN1 (r^2 = 0.76) was considerably higher than that of CAN2 (r^2 = 0.28). A plot of the canonical variate scores for each site (Fig. 2a) indicated that CAN1 mainly differentiated a bayhead community from those in willowheads and marshes, whereas CAN2 distinguished between bird communities in marshes and willowheads. Structure coefficients indicated that White-eyed Vireo, Red-bellied Woodpecker, and Northern Cardinal were more abundant in bayheads and these species best distinguished the bayhead community from those in the other vegetation types (Table 2). The Common Moorhen was more abundant in marshes and best distinguished that community from one in willowheads.

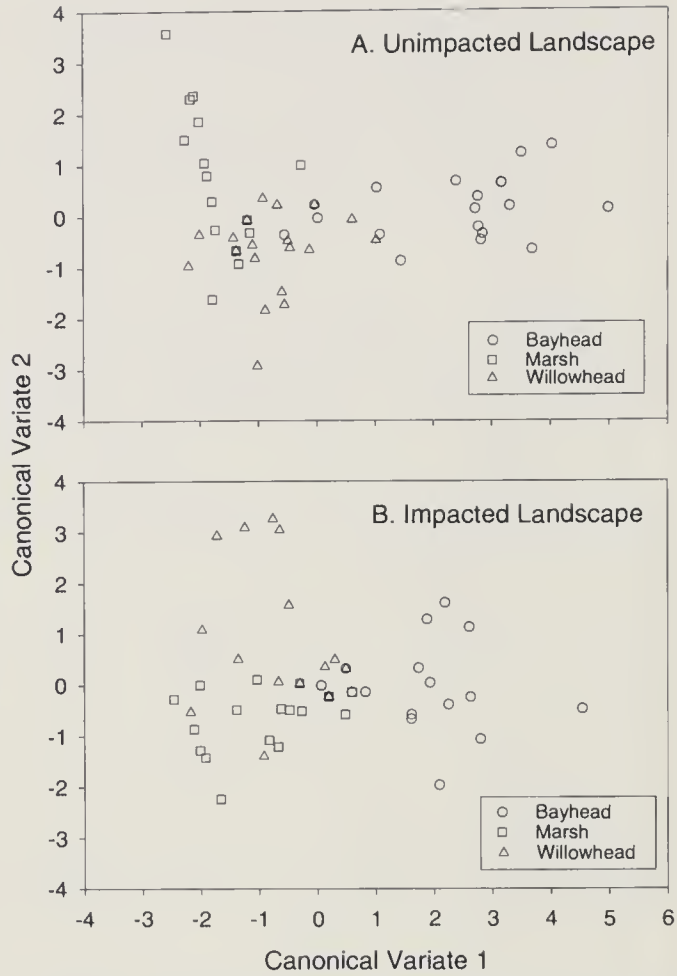

FIG. 2. Canonical variate scores based on avian abundance for sites in bayheads, willowheads, and marshes, in the (A) unimpacted landscape and (B) impacted landscape in the central Everglades, July–August 1996.

In the impacted landscape, bayhead communities were dominated by White-eyed Vireo, Red-winged Blackbird, Eastern Kingbird (*Tyrannus tyrannus*), and Boat-tailed Grackle, respectively (Table 1). Willowheads were dominated by Red-winged Blackbird, White-eyed Vireo, and Common Yellowthroat, respectively. The most abundant species in marshes were Red-winged Blackbird, Common Yellowthroat, and Common Moorhen, respectively.

The CVA in the impacted landscape indicated that the bayhead bird community was more similar to those of other vegetation types than it was in the unimpacted landscape. This finding was apparent from the lower canonical correlation coefficient of CAN1 in the impacted landscape (r^2 = 0.58) than in the unimpacted landscape and the similar canonical correlation coefficient of CAN2 in the impacted (r^2 = 0.30) and unimpacted landscape.

TABLE 2. Total structure coefficients for canonical variate analysis of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.[a]

Species	Unimpacted landscape		Impacted landscape	
	Canonical variate 1	Canonical variate 2	Canonical variate 1	Canonical variate 2
Anhinga[b]	—	—	−0.149	−0.260
Great Egret[b]	—	—	−0.149	−0.260
Green Heron	0.206	0.072	−0.158	0.514
Turkey Vulture	0.189	0.151	−0.143	0.072
Osprey	−0.066	−0.333	−0.111	0.360
Snail Kite[c]	−0.141	0.261	—	—
Red-shouldered Hawk[c]	0.279	0.097	—	—
Common Moorhen	−0.394	0.636	−0.394	−0.309
Yellow-billed Cuckoo[b]	—	—	0.090	0.237
Great Horned Owl[c]	−0.141	0.261	—	—
Red-bellied Woodpecker	0.553	0.097	0.309	0.141
Eastern Kingbird	0.364	0.126	0.565	−0.068
Carolina Wren[c]	0.206	0.072	—	—
Blue-gray Gnatcatcher	−0.066	−0.333	0.237	−0.028
Loggerhead Shrike[b]	—	—	0.305	−0.118
White-eyed Vireo	0.851	0.140	0.445	0.535
Common Yellowthroat	−0.188	−0.187	−0.204	−0.054
Northern Cardinal	0.525	−0.065	0.012	0.505
Red-winged Blackbird	−0.236	−0.247	−0.510	−0.067
Boat-tailed Grackle	0.454	−0.113	0.176	−0.239

[a] Total structure coefficient is the pairwise correlation between a canonical variate and a single variable.
[b] Rare species not included in the analysis of the unimpacted landscape.
[c] Rare species not included in the analysis of the impacted landscape.

A plot of the site scores (Fig. 2b) indicated that CAN1 mostly differentiated a bayhead community from those in the other vegetation types and CAN2 primarily distinguished between willowhead and marsh communities. Structure coefficients indicated that Eastern Kingbird, Red-winged Blackbird, and White-eyed Vireo distinguished the bayhead community from those in the other vegetation types (Table 2). Eastern Kingbird and White-eyed Vireo were more abundant in bayheads whereas Red-winged Blackbird was less abundant in bayheads than other vegetation types. White-eyed Vireo, Green Heron (*Butorides virescens*), and Northern Cardinal were more abundant in willowheads and best distinguished that community from one in marshes.

Species richness.—We detected 21 bird species at our sites over the course of the study (Table 1). Several additional species were seen during surveys or on travel between sites, but they did not meet our stated criteria for inclusion in the analysis. There was no significant difference ($P > 0.05$) in the number of species per survey between landscapes (Table 3). There was a significant difference ($P = 0.008$) in species richness among vegetation types but a significant interaction ($P = 0.02$) between landscape and vegetation type indicated that the differences among vegetation types were not consistent for both landscapes. Least significant difference tests revealed that in the unimpacted landscape, species richness was higher in bayheads compared to willowheads ($P = 0.004$) and marshes ($P < 0.001$). Whereas in the impacted landscape, there was no difference in species richness between any two vegetation types (all tests, $P > 0.05$). There was also no difference in species richness between marshes and willowheads in the unimpacted landscape ($P > 0.05$).

Total bird abundance.—Total abundance did not differ between landscapes ($P > 0.05$) nor among vegetation types ($P > 0.05$; Table 3). Bird abundance differed significantly across sampling periods ($P = 0.03$) and the interaction of sampling period × vegetation type × landscape ($P = 0.05$). However, because sampling period was included in our design to reduce unwanted variability rather than to provide inferences across time, we did not

TABLE 3. Split-plot ANOVA for bird abundance and species richness of birds in bayheads, willowheads, and marshes in the central Everglades, July–August 1996.

Source of variation	df	Bird abundance model		Species richness model	
		Mean square	*P*	Mean square	*P*
Landscape	1	12.3	0.25	0.28	0.70
Vegetation	2	19.3	0.13	11.6	0.008
Landscape × vegetation	2	27.0	0.06	9.23	0.02
Site (landscape × vegetation) (*Error A*)	23				
Sampling period	3	20.5	0.03	2.58	0.26
Landscape × sampling period	3	2.3	0.77	1.24	0.58
Vegetation × sampling period	6	7.4	0.33	1.78	0.48
Landscape × vegetation × sampling period	6	13.6	0.05	1.37	0.64
Site × sampling period (landscape × vegetation) (*Error B*)	69				

address differences in means. No other terms in the model were significant (all tests, $P > 0.05$).

DISCUSSION

Community composition.—Habitat specificity is a characteristic that makes a species useful for predicting future response to changes in landscape composition (i.e., a good indicator species; Weller 1995). However, this same trait is likely to make a species more vulnerable to changes in its respective habitat. The CVA allowed us to identify species most likely to be affected by changes in a particular vegetation type. For example, Common Yellowthroats and White-eyed Vireos were equally abundant when all sites were pooled (Table 1). However, the yellowthroat occurred in all vegetation types and was not indicative of any single habitat whereas the White-eyed Vireo was more abundant in bayheads and willowheads and largely defined the CANs associated with these two vegetation types.

Instances where species demonstrated habitat specificity based on the CVA, were usually consistent with our understanding of their general habitat requirements. For example, Red-bellied Woodpecker, Northern Cardinal, and White-eyed Vireo characterized bayheads or willowheads, and all these species are known to inhabit forests or brushy areas. The Osprey (*Pandion haliaetus*) was found exclusively in willowheads, which provided perch substrate and also frequently contained alligator holes that support the large fish Osprey prey upon. The Blue-gray Gnatcatcher's (*Polioptila caerulea*) association with willowheads in the impacted landscape was unusual. Although this species occurs in the Everglades during the breeding season (Stevenson and Anderson 1994) it is generally associated with larger trees than those found on willowheads. Thus, it is possible that the bird's association with willowheads in the impacted landscape reflected individuals foraging during migration.

Wading birds occurred in low abundances relative to other species and several species of wading birds that occur in the Everglades were absent from both our counts and those of earlier studies. Although this pattern may seem surprising given that the Everglades is often associated with large numbers of wading birds, few quantitative comparisons between wading birds and other avian species have been conducted. Also, the distribution of wading birds in the Everglades is closely linked to the distribution and depth of surface water (Bancroft et al. 1994, Hoffman et al. 1994). These factors often produce a very clumped distribution of birds with large portions of the marsh containing no birds at all and some portions of the marsh containing very high densities of birds. Finally, although the low numbers of wading birds we detected during the wet season reflects a real characteristic of the ecosystem, our 1.6-ha sampling plots are probably smaller than plots designed optimally to determine densities of only wading birds.

Historic community composition.—No quantitative bird community studies were conducted in the Everglades before drainage of the system began, thus we cannot get a complete assessment of how the avian community

has changed if indeed it has. In the southern Everglades, qualitative data (Robertson 1955) were collected in marshes and bayheads at the time the eastern perimeter levee of the Everglades was being constructed and before any of the WCAs were built (Light and Dineen 1994), and quantitative data (Kushlan and Kushlan 1977) were collected shortly after the WCAs were built. Comparison of species richness data from these earlier studies in Everglades National Park with data from the unimpacted landscape in this study provides some insight as to whether species richness has changed since the WCAs were built. However, because all these studies were conducted in slightly different areas, they may reflect some degree of spatial as well as temporal variability. Robertson (1955) reported 15 species, Kushlan and Kushlan (1977) reported 16 species, and we observed 16 species (excluding Tree Swallows) in the unimpacted landscape, indicating similar numbers of nesting species in the central and southern Everglades over a 40-year period. Most likely, none of the studies above recorded the presence of every species in the community because of the difficulty in accessing the Everglades interior and because of the large number of rare species present. Indeed, some differences in species composition among studies can be attributed to the presence of rare species showing up in one study but not in another. Two notable exceptions are Common Moorhen and White-eyed Vireo. Neither species was reported in the earliest studies in the southern Everglades (Robertson 1955, Kushlan and Kushlan 1977), but in our study, Common Moorhen was one of the most abundant marsh-species and White-eyed Vireo was one of the most abundant species in tree islands. Because these birds exhibited strong habitat associations, they contributed greatly to our ability to distinguish bird communities among vegetation types in the ordination.

We do not believe that the absence of Common Moorhen and Common Yellowthroat in earlier studies indicates that these species were absent from the Everglades during those times because both species were recorded in the southern Everglades during the 1960s (North American Breeding Bird Survey, unpubl. data). Two possible explanations for the marked differences in abundance of these two species between our study and earlier ones is that: (1) these two species have increased in abundance over time or (2) there are strong spatial differences with the two species being more abundant in the central Everglades than in the southern portions.

To further explore these hypotheses, we examined an independent data set consisting of one North American Breeding Bird Survey route conducted for 14 years from 1974–1994 in the east-central Everglades, and one route conducted for three years from 1983–1986 in the southern Everglades. These were the only routes that occurred completely within the Everglades. Spatial comparisons between routes revealed that for the Common Moorhen, the number of birds/survey was considerably higher at the northern route ($\bar{x}$ = 65, range 21–99, n = 14) than at the southern route ($\bar{x}$ = 1, range 0–2, n = 3). Whereas, the opposite was true for the White-eyed Vireo (northern route: $\bar{x}$ = 14, range 0–34, n = 14; southern route: $\bar{x}$ = 62, range 55–70, n = 3). To identify possible temporal changes in bird abundance we examined data from the northern route only and conducted a Spearman rank correlation test between the number of birds/survey and the year of survey. There was no significant trend in the abundance of the Common Moorhen over time ($r = -0.23$, $P > 0.05$, n = 14) but there was a significant increase in the White-eyed Vireo ($r = 0.85$, $P < 0.001$, n = 14). Collectively, patterns from the North American Breeding Bird Survey corroborate the differences in the abundance of Common Moorhen and White-eyed Vireo between our study and earlier ones in the southern Everglades. This independent data set suggests that the abundance patterns of the Common Moorhen reflect spatial differences between the northern and southern Everglades whereas the abundance patterns of the White-eyed Vireo may reflect increases over time.

Species richness.—Differences in species richness among vegetation types suggests that species richness was determined in large part at the habitat level (e.g., Mills et al. 1991, Craig and Beal 1992, Willson and Comet 1996). In the unimpacted landscape, we detected more species in bayheads, willowheads, and marshes, respectively, which was consistent with our initial prediction based on vegetation structure. However, the significant in-

teraction between landscape and vegetation type indicated that landscape characteristics also played a role in structuring the avian community. Strong differences in species richness among vegetation types were not evident in the impacted landscape. Our ordination identified a similar pattern with regard to species abundances. In the unimpacted landscape, we were better able to distinguish distinct avian communities among vegetation types than in the impacted landscape, where bird communities were more similar to one another.

The influence of landscape should be most important in open systems with small patches such that animals have to move among patches to find adequate resources (Wiens 1989b, Pearson 1993). Under these circumstances, the quality of one patch is less important than the average of all patches from which resources are obtained. This is likely the case for many bird species in the Everglades, particularly those with large home ranges such as wading birds and raptors. However, we also observed smaller birds such as Red-winged Blackbirds and Common Yellowthroats flying between tree islands or among vegetation patches within marshes. As compared to the unimpacted landscape, the impacted landscape has more cattail and shrub patches and a larger percentage of small tree islands. Thus, the small scale (several ha) diversity of patches within the marsh may have actually increased through past management practices, benefiting those species that are not adapted to obtaining resources from widely separated patches. Regardless of which species benefited from past management of the impacted landscape, the result is a collective avian community that differs from the one inhabiting the unimpacted region.

Our study demonstrates that in the central Everglades, two characteristics of a relatively unimpacted landscape are higher species richness in bayheads and a more distinct avian community in that vegetation type than in either willowheads or marshes. Although these characteristics are now absent in the impacted landscape, it is possible that restoration efforts aimed at restoring the historic vegetation communities at the landscape scale (South Florida Water Management District 1995) will restore avian community structure as well. Monitoring both structural characteristics of the avian community as well as population levels of key species will provide information on the success of the ecosystem restoration process.

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EFFECTS OF MALE REMOVAL ON FEMALE REPRODUCTIVE BIOLOGY IN ROSS' AND LESSER SNOW GEESE

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ABSTRACT.—We studied effects of mate removal on nesting and hatching success, incubation behavior, body mass, and post-hatch dispersal distance of female Ross' (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*) at Karrak Lake, N.W.T., Canada. Male geese were removed during early incubation (days 1–8), and widowed and paired control females were monitored through post-hatch dispersal. Nesting and hatching success did not differ between species or treatments (widowed vs paired) and averaged 77.5 ± 3.8% and 64.0 ± 3.6% (±SE), respectively. Paired females spent more time with their bills tucked (23.7 ± 3.3% vs 9.1 ± 4.0%) and less time alert (8.6 ± 2.9% vs 22.9 ± 3.5%) while on nests than did widowed females. Snow widowed females (31.1 ± 4.7%) and Ross' widowed females (20.6 ± 6.0%) generally spent more time each day in head-up alert than did Snow paired females (7.1 ± 3.8%), Snow paired males (11.8 ± 3.8%), Ross' paired females (9.4 ± 3.6%), and Ross' paired males (7.9 ± 3.6%). Body mass of paired and widowed female Ross' Geese did not differ at hatch or at time of post-hatch recapture; however, mean distance recaptured from the breeding colony was greater for paired (50.9 ± 6.1 km) than for widowed females (27.3 ± 6.6 km). Total mass gain (276 ± 19 g) and rate of mass gain (8.4 ± 0.5 g/day), from hatch until post-hatch recapture (33.1 ± 1.2 days), were similar for widowed and paired female Ross' Geese. Male removal experiments in monogamous, precocial species generally have produced few effects on female nesting success or incubation behavior. We suggest that male parental care in arctic-nesting geese is more critical during laying and the post-hatch period than during incubation. *Received 21 June 1996, accepted 29 June 1997.*

Swans and geese (Anserini), and whistling ducks (Dendrocygnini) form long-term pair-bonds in which both parents care for young. Perennial monogamy is associated with large body size, high probability of mate survival, lack of renesting opportunities, and obligate brood-rearing (Oring and Sayler 1992). Male geese defend territories and mates during incubation, and subsequently protect broods while females replenish nutrient reserves used during laying and incubation (Ryder 1975; Lazarus and Inglis 1978; Ankney 1977, 1979; Sedinger and Raveling 1990; Afton and Paulus 1992; Paine 1992). Arctic-nesting geese face ecological conditions that may favor extended male parental care, including colonial nesting, herbivory, and short breeding seasons (Martin et al. 1985, Gauthier and Tardif 1991, Oring and Sayler 1992). Although most geese pair for life, opportunities for extra-pair matings exist; thus, effective mate guarding and territorial defense by males should enhance their certainty of paternity and may deter predation. Consequently, mate loss, intrusion of other males, and costs of re-pairing reduce lifetime reproductive success (Owen et al. 1988, Forslund and Larsson 1990) and, therefore, could select for male attendance during incubation (Paine 1992).

Ross' (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*; hereafter Snow Geese) nest sympatrically in the central Canadian Arctic, providing a unique opportunity for comparative studies of similar species. Ross' Geese are smaller than Snow Geese [mean body mass of nesting adults (sexes combined) = 1356 g and 2029 g, respectively; MacInnes et al. 1989]. Daily energy requirements, clutch size, and vulnerability to predation are influenced by body mass via stored nutrient reserves (Barbault 1986). Female geese generally feed little during egg-laying and incubation, relying primarily on endogenous reserves to complete their clutches (Ryder 1970a, Ankney and MacInnes 1978). However, small species of geese (e.g., Ross' Geese) cannot store as much endogenous reserves as large species (but see Bromley and

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Jarvis 1993); consequently small species generally take more recess time during incubation to feed than do large species (Aldrich and Raveling 1983; Thompson and Raveling 1987; Afton and Paulus 1992; Afton, unpubl. data).

We investigated the importance of male Ross' and Snow Geese to nesting and hatching success, and to incubation behavior, body mass, and post-hatch dispersal of females. We predicted that widowed females would have lower nesting and hatching success than would paired females in both species. Snow Geese are larger and can store more nutrient reserves than can Ross' Geese; consequently, we reasoned that widowed Snow Geese would be capable of incubating for relatively longer periods and, therefore, should have greater success than should widowed Ross' Geese. We also predicted that behavior during incubation would differ between paired and widowed geese, if paired females benefit from mate-guarding. Benefits of male protection could include predator deterrence, reduced disturbance by neighboring females (i.e., nest parasitism), reduced harassment from males attempting forced extra-pair copulations, and increased foraging efficiency during incubation recesses. If male protection is beneficial during incubation, then paired females might be in better physiological condition at hatch than are widowed females. Finally, if parental care by male geese is important during brood rearing, then removing males at hatch should affect female condition, and gosling survival and growth. We predicted that if widowed females assumed sole responsibility for protecting their broods while concurrently replenishing nutrient reserves and molting, they would be in poorer condition than would paired females during the post-hatch period.

STUDY AREA AND METHODS

We studied Ross' and Snow Geese from 27 May to 9 August 1994 at Karrak Lake, N.W.T., Canada (67° 14′ N, 100° 16′ W). The area is typical tundra habitat with numerous shallow lakes and streams (Ryder 1972). Both species nest in areas of rock, heath, moss, or a mixture of these habitats located on islands or the mainland (McLandress 1983).

Nest selection.—We placed transects randomly through a 1-km^2 section of the colony located on the mainland and selected nests every 30 m along transects. We randomly selected species and direction from the transect (left or right) in which to select nests. A total of 120 nests (60 Ross', 60 Snow) were selected for the experiment and individually marked with small colored flags. We subsequently recorded final clutch size, embryo age (Weller 1956), and estimated first egg date (assuming a laying rate of 1 egg every 1.3 days for both species; Ryder 1970b). Each egg was numbered in several places and lines were drawn around the egg with a permanent marker to help determine hatching success (see below). Nests were observed every 3–5 days with a spotting scope to determine whether females were incubating their clutches. If a female was absent, we visited her nest immediately to determine condition of the clutch.

Nesting and hatching success.—After parents and broods left the colony, we estimated nesting and hatching success of all nests. A nest was classified as successful if at least 1 egg hatched. Hatching success was defined as percentage of eggs within a clutch that hatched. We classified an egg as hatched if any marked fragment (number or line) of eggshell, pieces of egg membrane, and/or gosling down were present in or near the nest.

Male removals.—Experimental nests were randomly assigned to one of two treatments: paired controls or widowed. Thirty-five nests of each species were allocated to control groups, and 25 nests of each species were assigned to widowed groups. Males assigned to the widow treatment were shot during early incubation (days 1–8) and used for other studies. We were unable to collect the entire sample of male Ross' Geese because of time constraints; consequently, we had 37 control and 23 widowed females for this species.

Incubation behavior.—We observed widowed and paired birds using focal-animal sampling techniques (Altmann 1974). We divided the day into 6 time periods: 00:01–04:00, 04:01–08:00, 08:01–12:00, 12:01–16:00, 16:01–20:00, and 20:01–24:00 CST. We randomly selected nests for observation during 2 of the 6 periods each day. We recorded activities of widowed females or paired females and their mates every 10 s during 15-min observation periods. Activities were categorized as alert (head-up or extreme head-up postures; Lazarus and Inglis 1978), foraging, walking, swimming, flying, comfort movements (preening, stretching, etc.; McKinney 1965), aggression (threats, calls, chases, and forced copulations), nest attendance (female only), and absent from territory. Behavior of females while on nests was subdivided into 4 categories: head-low (non-alert behavior; Lazarus and Inglis 1978), alert (head-up or extreme head-up), bill-tucked, and comfort movements.

Body mass and dispersal distance of female Ross' Geese.—We trapped a random sample of paired control females (N = 16) at the end of incubation (days 21–23) to compare body mass with that of widowed females. Females were captured using remote-controlled, modified bow-net traps (B. M. Grand, pers. comm.). Widowed females (N = 10) were shot at days 22–23 of incubation and used for other studies. All trapped and collected geese were weighed (±1 g) and

measured (mid-wing, tarsus bone, and head length; ±0.1 mm; Dzubin and Cooch 1992).

We attached radio transmitters to random samples of paired control females (n = 16) and paired females whose mates subsequently were removed at hatch (n = 13) to obtain post-hatch dispersal distances. Transmitters weighed an average of 26 g and were attached using a modified backpack harness (Dwyer 1972). Captured females also were fitted with neck collars and standard leg bands. Goslings (n = 33 of paired control females, n = 32 of females widowed at hatch) were web-tagged through the eggshell during the pipping stage (Alliston 1975) or at hatch using metal web-tags to allow comparisons of gosling growth and survival rates. Geese were relocated 29–42 days after hatch using telemetry; aerial antennae were mounted on a helicopter, and flightless geese were captured by driving them into a portable net corral. Females and web-tagged goslings were banded, collared, weighed and measured. Recapture distance from the breeding colony was determined using a Global Positioning System. As a result of time, permit and funding constraints, we were unable to trap, radio track or collect female Snow Geese for analysis of body mass and dispersal distance.

Statistical analysis.—We used analysis of variance (ANOVA) to test for differences in first egg date, clutch size, predicted hatch date, and hatching success between species, treatments, and their interaction (Proc GLM, SAS Institute 1990). We compared least-square means (LSM) using t-tests when sample sizes were unequal (PDIFF option, SAS Institute 1990) and used Tukey's studentized range test to compare unadjusted means when sample sizes were equal (Sokal and Rohlf 1981). Because of time constraints, we were unable to accurately estimate first egg date for 18 of the 120 experimental nests. These included four paired Ross', five widowed Ross', three paired Snow, and six widowed Snow Goose nests. Accordingly, these nests were excluded from analyses of first egg date and predicted hatch date.

We tested whether nest success differed between species, treatments, and their interaction using maximum-likelihood ANOVA (Proc CATMOD, SAS Institute 1990). We present apparent nest success (number of successful nests/total nests) because we began monitoring all nests during early laying. We also used maximum-likelihood ANOVA to test whether number of nests that had partial clutch reduction during incubation (but still hatched ≥1 egg) differed between species, treatments or their interaction.

We computed proportion of time spent in various behavioral activities by dividing the frequency that each behavior was recorded by the maximum number of behaviors possible per 15-min sampling period (n = 90). We analyzed raw and arcsine square-root transformed proportions (Sokal and Rohlf 1981) using multivariate analysis of variance (MANOVA) to examine differences in overall time-activity budgets by species, treatment, stage of incubation, and associated interactions. Stage of incubation was divided into 3 categories: early (days 1–8), mid (days 9–15), and late (days 16–23). We used means of behavioral observations for the few nests that were observed more than once. Significant explanatory variables from MANOVA were used in ANOVAs to examine effects on individual behaviors. For females, four behaviors were used in the analysis: nest attendance (i.e., incubation constancy), foraging, absent from territory, and alert posture (while off nests). These behaviors accounted for more than 98% of female activities. We further analyzed head posture of females while on nests (head-low, comfort movements, bill-tucked, and alert). In addition, we compared time spent alert (head-up or extreme head-up) each day among experimental female groups (k = 4 groups) and male geese (k = 2). We compared LSMs in behavioral analyses because of unbalanced designs (PDIFF option, SAS Institute 1990). Analyses of raw and transformed proportion data yielded similar results in final models; therefore, we report results from analyses of raw data (LSM ± SE).

Because body mass often is related to structural size and body size is positively correlated with post-hatch dispersal distance in Ross' Geese (Slattery 1994), we indexed female body size using Principal Components Analysis (PCA; Proc PRINCOMP, SAS Institute 1990). Body size was defined as the first principal component (PC1) computed from the correlation matrix of mid-wing, tarsus bone, and head length measurements. We ran separate PCAs to estimate body size for females at hatch and during post-hatch dispersal; all loadings were positive and explained 80–84% of the original cumulative variance.

We used analysis of covariance (ANCOVA) to test for differences in body mass and post-hatch dispersal distance between treatments, with PC1 (i.e., body size) used as a covariate in models. We used ANCOVA to test for differences in mass change (from hatch to post-hatch recapture) between treatments, with days elapsed since hatch, recapture distance, and PC1 as covariates. We also used ANCOVA to test for differences in rate of mass change between treatments, with recapture distance and PC1 as covariates. Pearson correlation coefficients (r) were used to describe relationships between PC1 and various response variables (Proc CORR, SAS Institute 1990). Finally, we tested for statistical significance of the combined results of ours and other goose studies, to determine whether nest success of widows was lower than that of controls, using Fisher's inverse χ^2 method (Hedges and Olkin 1985:37).

RESULTS

First egg date, clutch size, and predicted hatch date.—First egg date did not differ between species (F = 2.82; df = 1, 98; P > 0.05) or treatments (F = 0.62; df = 1, 98; P > 0.05); the species-by-treatment interaction also was not significant (F = 0.52; df = 1, 98; P > 0.05). Modal first egg date for Ross'

TABLE 1. Fate of experimental nests at Karrak Lake, N.W.T., Canada, 1994.

	Ross' Geese				Snow Geese			
	Control		Widow		Control		Widow	
Fate of nest	n	%	n	%	n	%	n	%
Unsuccessful[a]	7	18.9	8	34.8	6	17.1	6	24.0
Successful	30	81.1	15	65.2	29	82.9	19	76.0
Clutch reduction[b]	8	21.6	3	13.0	9	25.7	6	24.0
Total nests[c]	37		23		35		25	

[a] Nests abandoned, or preyed upon and entire clutch lost.
[b] Reduction occurred during incubation, but ≥1 egg hatched in nest.
[c] Unsuccessful + successful nests.

(39% of 51 nests) and Snow Geese (41% of 51 nests) was 31 May.

Mean clutch size of Snow Geese (3.95 ± 0.08; n = 60) was larger (F = 16.64; df = 1, 116; P < 0.001) than that of Ross' Geese (3.43 ± 0.08; n = 60), but the treatment main effect (F = 0.14; df = 1, 116; P > 0.05) and treatment-by-species interaction were not significant (F = 0.64; df = 1, 116; P > 0.05).

Predicted hatch date did not differ between species (F = 0.01; df = 1, 98; P > 0.05) or treatments (F = 1.25; df = 1, 98; P > 0.05), and the species-by-treatment interaction also was not significant (F = 0.18; df = 1, 98; P > 0.05). Modal predicted hatch date for Ross' (55% of 51 nests) and Snow Geese (45% of 51 nests) was 27 June. First egg and predicted hatch dates were 8–16 days earlier in 1994 as compared to previous years (1991–1993) at Karrak Lake (Slattery and Alisauskas 1993).

Nesting and hatching success.—Nesting success did not differ between species (χ^2 = 0.53, df = 1, P > 0.05) or treatments (χ^2 = 1.98, df = 1, P > 0.05); the species-by-treatment interaction also was not significant (χ^2 = 0.21, df = 1, P > 0.05; Table 1). Nesting success for both species combined was 77.5 ± 3.8% (N = 120). Nests with partial clutch reduction did not vary by species (χ^2 = 1.04, df = 1, P > 0.05) or treatments (χ^2 = 0.54, df = 1, P > 0.05), and the species-by-treatment interaction was not significant (χ^2 = 0.29, df = 1, P > 0.05; Table 1).

Hatching success did not differ between species (F = 0.12, df = 1, 116, P > 0.05) or treatments (F = 0.12, df = 1, 116, P > 0.05); the species-by-treatment interaction also was not significant (F = 0.10, df = 1, 116, P > 0.05). Hatching success for both species combined averaged 64.0 ± 3.6% (N = 120).

Female behavior during incubation.—We collected focal-animal samples from 44 female Ross' (n = 27 control, 17 widow) and 46 female Snow Geese (n = 27 control, 19 widow) during incubation. Overall percent time spent in nest attendance, alert (off nest), absent from territory, and foraging by females did not differ between species (F = 0.50; df = 4, 129; P > 0.05) or treatments (F = 1.38; df = 4, 129; P > 0.05), or among incubation stages (F = 1.60; df = 8, 258; P > 0.05; Table 2); none of the interactions of various main effects were significant (all P > 0.05). Nest attendance for both species combined averaged 91.8 ± 3.0%.

Head postures of incubating females differed between treatments (F = 4.72; df = 4, 130; P < 0.002) and among incubation stages (F = 3.09; df = 8, 260; P < 0.003), but were similar between species (F = 0.80; df = 4, 122; P > 0.05); none of the interactions were significant (all P > 0.05). Paired females spent more time with their bills tucked (F = 8.32; df = 1, 133; P < 0.005), and less time alert while on nests than did widows (F = 10.62; df = 1, 133; P < 0.002; Table 2). Time spent with bill tucked under the wing differed among incubation stages (F = 9.32, df = 2, 133, P < 0.001). Females spent more time with bill tucked during late incubation than during early or mid incubation (Table 2).

Alert behavior of males and females.—Overall time spent alert each day differed among control Ross' females, widowed Ross' females, control Snow females, widowed Snow females, Ross' males, and Snow Goose males (F = 3.08; df = 10, 390; P < 0.001); however, stage of incubation (F = 0.96; df = 4, 390; P > 0.05) and stage-by-group interaction were not significant (F = 0.99; df =

TABLE 2. Percent time spent in various behaviors (least-square means ± SE) by species, treatment, and incubation stage for female geese at Karrak Lake, N.W.T., Canada, 1994.

Category	n	Analysis of on-nest behaviors				Analysis of off-nest behaviors		
		Head-low	Alert	Bill-tucked	Comfort	Feeding	Absent	Alert
Species								
Ross'	44	59.8 ± 4.8A[a]	13.5 ± 3.2A	15.0 ± 3.6A	0.6 ± 0.1A	1.3 ± 0.7A	6.4 ± 2.6A	0.5 ± 0.4A
Snow	46	57.4 ± 4.7A	17.9 ± 3.1A	17.7 ± 3.6A	0.5 ± 0.1A	0.3 ± 0.6A	4.3 ± 2.5A	0.5 ± 0.4A
Treatment								
Control	54	59.4 ± 4.3A	8.6 ± 2.9B	23.7 ± 3.3A	0.4 ± 0.1A	1.5 ± 0.6A	3.7 ± 2.3A	0.7 ± 0.4A
Widow	36	57.7 ± 5.2A	22.9 ± 3.5A	9.1 ± 4.0B	0.7 ± 0.2A	0.2 ± 0.2A	7.0 ± 2.8A	0.4 ± 0.5A
Stage								
Early	26	55.4 ± 7.4A	17.9 ± 4.9A	13.6 ± 5.7B	0.8 ± 0.2A	0.2 ± 1.1A	7.5 ± 4.0A	0.2 ± 0.2AB
Mid	63	66.2 ± 4.7A	15.2 ± 3.1A	5.9 ± 3.6B	0.3 ± 0.1A	0.8 ± 0.7A	8.7 ± 2.5A	1.2 ± 0.5A
Late	47	54.0 ± 5.4A	14.2 ± 3.6A	29.7 ± 4.2A	0.5 ± 0.2A	1.4 ± 1.1A	4.6 ± 2.9A	0.1 ± 0.1B

[a] Within an analysis, least-square means with different letters within a category and behavior are significantly different ($P < 0.05$).

TABLE 3. Percent time spent in head-up alert (least-square means ± SE) during incubation by experimental group at Karrak Lake, N.W.T., Canada, 1994.

Group	n	Head-up
Ross' widow females	28	20.6 ± 6.0AB[a]
Snow widow females	32	31.1 ± 4.7A
Ross' paired females	40	9.4 ± 3.6C
Snow paired females	37	7.1 ± 3.8C
Ross' paired males	40	7.9 ± 3.6C
Snow paired males	37	11.8 ± 3.8BC

[a] Least-square means with different letters are significantly different ($P < 0.05$).

20, 390; $P > 0.05$). Time spent head-up alert each day differed among groups ($F = 4.42$; df = 5, 196; $P < 0.001$), whereas time spent in extreme head-up alert was similar among groups ($F = 1.40$; df = 5, 196; $P > 0.05$) and averaged 0.9 ± 0.2%. Widowed Ross' and Snow Goose females generally spent more time in head-up alert than did geese in other groups (Table 3).

Body mass and post-hatch dispersal distance of female Ross' Geese.—Body mass at hatch was positively ($r = 0.54$) related to PC1 ($F = 9.48$; df = 1, 23; $P < 0.006$), but mass did not differ ($F = 0.01$; df = 1, 23; $P > 0.05$) between paired (995 ± 18 g, $n = 16$) and widowed females (997 ± 23 g, $n = 10$). Overall mean mass at hatch, unadjusted for size, was 996 ± 16 g ($n = 26$).

Because of limited helicopter time, we captured only 13 radio-tagged females (5 paired controls, 8 widowed at hatch). Only one female (paired control) recovered in banding drives had web-tagged goslings ($n = 2$ out of 4 goslings hatched); one other control female escaped before being weighed. Body mass at recapture was positively ($r = 0.82$) related to PC1 ($F = 19.22$; df = 1, 9; $P < 0.002$), but mass did not differ ($F = 0.07$; df = 1, 9; $P > 0.05$) between paired (1266 ± 40 g; $n = 4$) and widowed females (1279 ± 28 g; $n = 8$). Overall mean mass at recapture was 1275 ± 37 g ($n = 12$).

Mass change of females was not related to days elapsed since hatch (33.1 ± 1.2 days, Range = 29–42 days, $n = 12$; $F = 0.20$; df = 1, 7; $P > 0.05$), recapture distance ($F = 0.01$; df = 1, 7; $P > 0.05$) or PC1 ($F = 0.75$; df = 1, 7; $P > 0.05$), and mass change did

TABLE 4. Summary of studies investigating the influence of male removals on reproductive parameters in precocial birds.

Species (Citation)	Impact of Male-removal				
	Nest success	Brood survival	Brood growth	Female survival	Female body mass
Lesser Snow Geese (Martin et al. 1985)	Varied[a]	Varied[b]	—[c]	—	Decline
Bar-headed Geese (Schneider and Lamprecht 1990)	—	Decline	NS[d]	—	—
Canada Geese (Paine 1992)	NS	Decline	—	—	NS
Wood Duck (Hipes and Hepp 1993)	NS	—	—	—	—
Willow Ptarmigan (Hannon 1984)	Varied[e]	NS	—	Decline	—
Willow Ptarmigan (Martin 1984)	—	—	—	NS	Increase
Willow Ptarmigan (Martin and Cooke 1987)	NS	NS	—	NS	Varied[f]
Western Sandpiper (Erckmann 1983)	Decline	—	—	—	—
Ross' Geese (This study)	NS	—	—	—	NS
Lesser Snow Geese (This study)	NS	—	—	—	—

[a] At Boas River, paired females had higher ($P < 0.001$) nest success than did widows whose mates were removed during early laying, but nest success was similar when males were removed during late laying ($P > 0.051$) and during incubation ($P > 0.056$). At La Perouse Bay, nest success was similar for paired females and widows whose males were removed in early incubation ($P > 0.05$).
[b] Suggested decline at La Perouse Bay in 1983, but no difference in 1984.
[c] Data not collected.
[d] Data not significant.
[e] Nest success declined in 1981, but did not differ in 1979 and 1980.
[f] Widows were heavier than paired females at hatch in 1982; trends in 1981 and 1983 were similar, but not significantly different. Widows lost more weight than did paired females in the post-hatch period.

not differ ($F = 0.31$; df = 1,7; $P > 0.05$) between paired (282 ± 58 g; $n = 4$) and widowed females (273 ± 12 g; $n = 8$). Mass change averaged 276 ± 19 g (Range = 192–448 g; $n = 12$) for all females combined. Rate of mass change was not related to recapture distance ($F = 0.03$; df = 1, 8; $P > 0.05$) or PC1 ($F = 1.18$; df = 1, 8; $P > 0.05$), and did not differ between paired (7.5 ± 1.2 g/day; $n = 4$) and widowed females (8.8 ± 0.7 g/day; $n = 8$; $F = 0.75$; df = 1, 8; $P > 0.05$). Overall rate of mass gain averaged 8.4 ± 0.5 g/day (Range = 5.1–10.7 g/day; $n = 12$). Distance recaptured from the colony was not related to PC1 ($F = 1.42$; df = 1, 10; $P > 0.05$), but paired female Ross' Geese (50.9 ± 6.1 km; $n = 5$) were recaptured further ($F = 7.54$; df = 1, 10; $P < 0.021$) from the colony than were widowed females (27.3 ± 6.6 km; $n = 8$).

DISCUSSION

Female reproductive success.—We predicted that removal of male Ross' and Snow Geese during early incubation would negatively affect several components of female reproductive success. However, we did not detect statistically significant differences in nesting or hatching success between treatments, although nest success varied in the predicted directions for both species (Table 1). Simulation modeling indicated that sample size would have to be doubled (i.e., 120 nests for each species) in order for observed estimates of nest success to be statistically different ($P < 0.05$). Other male removal studies in precocial species also detected little or no differences in nest success between widowed and paired females (Table 4). However, among the 6 statistical tests on geese, nest success varied in the predicted direction in 4 tests and was significantly different in 1 test. Meta-analysis of combined P-values from the 6 tests indicated a significant overall difference between treatments ($\chi^2 = 23.11$, df = 12, $P = 0.0268$); however, when the P-value from the single significant test was excluded, the combined analysis was not significant ($\chi^2 = 9.30$, df = 10, $P > 0.05$). Martin et al. (1985) also reported that rates of egg loss or intraspecific nest parasitism did not differ between widowed and paired Snow Geese breeding at a smaller sub-arctic colony.

Several factors may explain why male removals during incubation have little or no effect on nest success in colonial geese. By early incubation, territories have been established, laying is completed, and females can no longer be fertilized via extra-pair copulations (EPCs). Accordingly, forced EPCs rarely occurred during incubation at Karrak Lake (LeSchack, unpubl. data; Afton, unpubl. data;

but see Mineau and Cooke 1979). Paine (1992) rejected the hypothesis that non-colonial Canada Goose females benefit from male protection against predators; however, he questioned his results because nest success was high (>82%) and many males frequently were away from their nests.

We found that early snow melt at Karrak Lake did not result in increased overall nest success. Although egg-laying began 8–16 days earlier than in the previous three years, nest success of Ross' (75%) and Snow Geese (80%) were similar to rates recorded at Karrak Lake in 1993 (82% Ross', 76% Snow; Slattery and Alisauskas 1993). Adverse weather conditions upon arrival at breeding grounds delay reproduction and reduces clutch size. Atlantic Brant (*Branta bernicla hrota*) expended more energy searching for nest sites and food resources, and had lower productivity when nesting was delayed by late snow melt (Barry 1962). We suggest, that during a delayed breeding season, widowed females might have significantly lower nest success than do paired females as a result of declines in physiological condition caused by an increase in energy expenditure. Widows also might take more or longer incubation recesses than would paired females during late breeding seasons to search for food, thereby increasing the risk of both nest predation and a lengthened incubation period (Aldrich and Raveling 1983, Madsen et al. 1989). We observed that time spent off nests by widowed and paired females of both species, although not statistically different, varied in the predicted direction even though it was an early breeding season. We suspect that our sampling effort was not adequate to detect small differences in reproductive success that could impinge on fitness differences between treatment groups.

Incubation behavior, body mass and post-hatch dispersal distance.—In our study, nest attendance of Ross' and Snow Geese during early incubation was similar to that recorded in June 1993 at Karrak Lake (Afton, unpubl. data). Others who did male removal experiments in Snow Geese (Martin et al. 1985) and Canada Geese (Paine 1992) reported no differences in incubation constancy between widowed and paired geese. However, widows were harassed and displaced more often than paired females (Martin et al. 1985, Schneider and Lamprecht 1990). We also found that nest attendance was similar between widowed and paired females, although the trend was in the predicted direction. Similar trends also were reported for Snow Geese (Martin et al. 1985) and Canada Geese (Paine 1992).

We found that presence of their mates resulted in paired females spending more time with their bills tucked and less time alert while on nests than did widowed females. Widowed female Snow Geese spent twice as much time in the extreme head-up posture while incubating compared to paired individuals (Martin et al. 1985). A similar observation was reported for widowed Canada Geese (Paine 1992). Martin et al. (1985) suggested that an increase in alert behavior might result in an energy cost (i.e., decrease in body mass) to widowed birds. We did not detect a significant difference in body mass at hatch between paired and widowed female Ross' Geese, although the trend was in the predicted direction; however, our sample size was small. Body mass of widowed ptarmigan also did not differ from that of paired females at the end of incubation (Martin 1984).

Our study is the first to examine effects of male removal on post-hatch dispersal distance. Paired Ross' females were recaptured nearly twice as far from the breeding colony as were widowed females. We suggest that paired females are able to travel further and to better brood-rearing areas than are widowed females because of presence of their mates; however, this hypothesis needs to be tested. Slattery (1994) found that body size of Ross' Geese varied positively with recapture distance from the breeding colony at Karrak Lake; however, we found no relationship between body size and recapture distance. Thus, pair status appears more important than body size in determining post-hatch dispersal from the colony.

Role of male geese in biparental care.—Male removal experiments in monogamous, precocial species generally have produced few effects on nest success or female incubation behavior. In our study, widowed female geese spent increased time alert while on nests, but this apparently did not entail major physiological costs because body mass at hatch was similar for paired and widowed females.

We suggest that male parental care in Arctic-nesting geese is more critical during laying than during incubation. Removal of males during laying may cause many females to abandon nests because of increased sexual and physical harassment (e.g., forced EPCs) from conspecifics. Nest success differed between widowed and paired Snow Geese in a subarctic colony when males were removed during early laying (eggs 1–2; Martin et al. 1985). Lone Snow Goose females were subjected to frequent harassment from neighboring males (Martin et al. 1985); however, these authors did not determine whether this directly caused nest failure.

We also suggest that male parental care is more critical after hatch than during incubation because males are primary providers of brood defense while females replenish nutrient reserves utilized during laying and incubation (Ankney 1977, 1979; Lazarus and Inglis 1978; Sedinger and Raveling 1990; Afton and Paulus 1992). Female geese lose 11–32% of their body mass during incubation (Ankney and MacInnes 1978, Aldrich and Raveling 1983, Thompson and Raveling 1987, Afton and Paulus 1992). Brood survival generally is reduced by male removal (Table 4). For example, Schneider and Lamprecht (1990) reported higher gosling feeding and survival rates and fewer interruptions of brooding for paired females than for widows in a semicaptive flock of Bar-headed Geese (*Anser indicus*). We conclude that, under normal breeding conditions, male removal during incubation is not greatly detrimental to nest success or female body condition; however, effects of male removal during incubation in a late nesting season should be studied. Finally, we believe that future research should focus on the importance of biparental care during the laying and post-hatch periods.

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INTERBREEDING OF ROSEATE AND ARCTIC TERNS

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ABSTRACT.—This study provides evidence for hybridization between Roseate (*Sterna dougallii*) and Arctic (*S. paradisaea*) Terns. I observed a male Arctic and female Roseate Tern engaging in courtship, copulation, incubation and chick-feeding behavior on Country Island, Nova Scotia, Canada in 1996. The Roseate laid a single egg which hatched after 21 days. The chick, which I banded after hatch and weighed every other day, survived for 16 days before it was presumed depredated. The chick most resembled an Arctic Tern because its down lacked the spiny texture of Roseate chicks and it did not develop the dark, U-shaped dorsal markings characteristic of juvenile Roseates. The feeding rate for the mixed-species pair was below the mean, but within the range, of feeding rates for Roseate pairs at Country Island in 1996. The hybrid chick initially grew at the same rate as other Roseate chicks at this colony, but its growth slowed after 9 days such that it weighed less than all Roseate chicks under study. A skewed sex ratio, misimprinting on heterospecific vocalizations or parental inexperience may have led to this mating. *Received 15 March 1997, accepted 27 Oct. 1997.*

Hybridization is known to occur in roughly 10% of all bird species (Grant and Grant 1992). In some groups hybridization is rare, while in others it is quite common. For example, 9 of 23 tern species (family: Laridae) that breed in Europe and North America are known or believed to hybridize with one or more sympatric species (Table 1).

Matings between Roseate Terns (*Sterna dougallii*) and Common Terns (*S. hirundo*) have been well documented in both Europe and North America (Robbins 1974, Hays 1975, Zingo et al. 1994). In contrast, hybridization between Roseate and Arctic Terns (*S. paradisaea*) has apparently not been described, perhaps because these species are sympatric only over a narrow range (Cramp 1985). Roseate and Arctic Terns have been observed sharing incubation on two previous occasions (in Shetland, Scotland and Maine, U.S.A.; Ewins 1987; S. Kress, pers. comm.), but in both cases copulation was not observed and chicks were not found.

I studied the nesting behavior of Roseate Terns on Country Island, Nova Scotia, Canada in 1996, and witnessed hybridization between a Roseate and Arctic Tern. Here, I document the courtship, copulation, incubation and chick-feeding behavior of the mixed species pair, as well as the appearance, behavior and growth of the hybrid chick. I discuss some proximate mechanisms that may have led to this mating, as well as conservation implications of hybridization for Roseate Terns.

METHODS

Country Island is a 19 ha island located in Guysborough County, Nova Scotia (45° 06′ N, 61° 32′ W). Arctic (330 pairs), Roseate (45–50 pairs) and Common (130 pairs) terns nest on the south end of the island on rocky beach and in tall vegetation dominated by seaside angelica (*Coelopleurum lucidum*), swamp buttercup (*Ranunculus septentrionalis*), beach pea (*Lathyrus japonicus*), raspberry (*Rubus* spp.), and various sedges (*Carex* spp.) and grasses (Family: Gramineae). Great Black-backed Gulls (*Larus marinus*), Herring Gulls (*Larus argentatus*), American Crows (*Corvus brachyrhynchos*), Common Ravens (*Corvus corax*), Common Eiders (*Somateria mollissima*), Leach's Storm Petrels (*Oceanodroma leucorhoa*) and various songbirds and shorebirds also nest on the island. Gull predation on tern chicks is high (more than 50% of all tern chicks were depredated by gulls in 1996; Whittam, unpubl. data), but there are no resident mammalian predators.

A co-worker and I observed the male Arctic and female Roseate Tern with 8×36 binoculars and a spotting scope from two blinds located approximately 40 m from the nest and from a tower blind located on the edge of the colony (60 m from the nest). We observed courtship behavior of the pair for a total of 99 hours between 31 May and 11 June. During incubation (11 June–2 July) no formal observations were made but we checked the nest daily from the blinds to ensure the parents were incubating. From 3–18 July we observed the parents feeding the chick for a total of 42.5 hours. Observation periods were two to four hours long and occurred between 05:00 and 19:30 AST throughout courtship and chick-feeding.

Although neither the Roseate nor the Arctic Tern was color banded, I am confident that repeated observations were of the same two individuals because we saw them consistently in a single location. Both terns

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TABLE 1. Evidence for hybridization between some tern species (Family: Laridae).

Species believed to hybridize	Evidence	Reference(s)
Black Tern (*Chlidonias niger*) & White-Winged Black Tern (*C. leucopterus*)	Juveniles with mixed plumage characteristics	Vinicombe 1980 Davis 1982
Common Tern (*Sterna hirundo*) & Arctic Tern (*S. paradisea*)	None given	Degland and Gerbe 1867 (in Hays 1975)
Common Tern & Roseate Tern (*S. dougallii*)	Mixed-species copulation, incubation and chick-feeding behavior; chicks with mixed plumage characteristics	Robbins 1974 Zingo et al. 1994 (and references therein)
	Adults with intermediate plumage characteristics	Hays 1975
Roseate Tern & Arctic Tern	Mixed-species incubation	Ewins 1987 S. Kress, pers. comm.
	Mixed-species copulation, incubation and chick-feeding behavior; chick with mixed plumage characteristics	This paper
Gull-billed Tern (*Gelochelidon nilotica*) & Forster's Tern (*S. forsteri*)	None given	Hill 1965
Lesser Crested Tern (*S. bengalensis*) & Sandwich Tern (*S. sandvicensis*)	Mixed-species pairs	Brichetti and Foschi 1987
	Juveniles with intermediate plumage characteristics	Steele and McGuihan 1989 Verroken 1990

appeared typical of their respective species. I photographed the egg and chick using a 35 mm SLR camera equipped with a 50 mm focal length lens, and I measured the length and width of the egg with calipers. I used a spring scale to weigh the hybrid as well as 30 Roseate chicks beginning at hatch and continuing every other day until the chicks died or disappeared. I calculated the rates at which both parents fed the hybrid. Mean values are expressed ±1 SE.

RESULTS AND OBSERVATIONS

I first saw the Roseate and Arctic Tern posturing (in both the "bent" and "erect" positions; Cramp 1985) on 31 May in an area dominated by other courting Roseate Terns. The male Arctic mounted the female Roseate on the mornings of 31 May, 1 June and 2 June but cloacal contact did not occur. On 1 June the Roseate landed beside the Arctic, postured and gave begging calls. The pair was engaged in nest-shaping behavior (Cramp 1985) on 2 June. I observed two mate-feedings on 3 June, and on 5 June the Arctic mounted the Roseate and achieved cloacal contact. I observed four additional mountings on 6 June, two of which resulted in cloacal contact. The fourth mounting was preceded by the Arctic giving the Roseate a small fish, which they passed back and forth five times before it was swallowed by the Roseate. I observed two further instances of both mate-feeding and copulation on 8–9 June. The Roseate was seen arranging nest material from 9–11 June.

A single egg was found at the nest on 11 June, one day after the modal date of clutch initiation for other Roseates nesting at this colony (Whittam, unpubl. data). Thirty-five percent (n = 46) of Roseate nests on Country Island in 1996 contained one egg (Whittam, unpubl. data). The egg, which was highly elongate and pyriform (49 × 28 mm; Fig. 1), differed from both Roseate and Arctic Tern eggs (Table 2). The nest was in dense raspberry and seaside angelica. The nearest nest (1.1 m away) belonged to a pair of Roseate Terns, although three pairs of Common Terns also nested within 2 m. The nearest Arctic Tern nest was approximately 18 m away.

Both the Arctic and Roseate terns incubated the egg. I trapped the Arctic Tern on the nest using a drop-style treadle trap on 30 June, photographed it, and banded it (U.S. Fish and

FIG. 1. Egg of interbreeding Roseate and Arctic Tern.

Wildlife Service #811-26033). The Roseate began incubating four minutes after the Arctic Tern was removed from the trap. The egg hatched on 2 July, after a 21 day incubation period (Table 2), which was two days shorter than the mean incubation period for 27 Roseate Tern eggs on Country Island in 1996 (mean = 23.4 ± 0.9 days, range = 22–25; Whittam, unpubl. data).

I banded the chick (#802-68-342) two days after hatching, and photographed it 2, 6, and 15 days after hatching. The plumage of the

TABLE 2. Egg, chick and fledgling characteristics of Roseate[a] and Arctic[a] Terns and of the hybrid Roseate × Arctic Tern.

Characteristic	Arctic	Roseate	Hybrid
Mean egg length × width (mm)	41 × 30 range 36–46 × 26–33 (n = 300)	43 × 30 range 38–48 × 27-32 (n = 180)	49 × 28
Incubation period (days)	20–24	21–26	21
Texture of chick down	soft	spiny	soft
Color of chick down	pearl grey or buff	cinnamon buff to pale buff, or pale grey to off-white	cinnamon buff
Plumage markings of chick	usually dense black specks or streaks	usually diffuse black-brown specks	large black spots and streaks
Fledgling plumage	mantle, scapulars and tertials light grey with off-white tips and dark grey subterminal spots	black U-shaped markings on mantle/back feathers and tertials	no distinctive marks at 15 days
Fledgling bill color	orange tipped with black	black	flesh-colored, tipped with black at 15 days
Fledgling leg color	orange-red	black	purplish brown at 15 days

[a] From Cramp (1985) and Malling Olsen and Larsson (1995).

FIG. 2. Hybrid Roseate × Arctic chick (on right) and Roseate Chick (on left) at two days of age.

chick lacked the characteristic spiny texture of Roseate chicks (Cramp 1985; Fig. 2), and it never developed the dark, U-shaped markings on the mantle, back and tertials which are characteristic of juvenile Roseate, but not Arctic, Terns (Malling Olsen and Larsson 1995). The color and markings of the chick's down resembled those of both Arctic and Roseate chicks, and at 15 days the chick's purplish brown legs and flesh-colored bill were intermediate in appearance between those of Arctic and Roseate fledglings (Table 2).

The Arctic brought 60% (n = 53) of all fish to the chick. Male Arctic Terns generally bring more food to the nest than do females, especially during the first week after hatching (Uttley 1992). The size of prey brought to the nest by the Roseate and Arctic Tern did not differ (mean fish size = 1.15 ± 0.12 and 1.18 ± 0.10 bill lengths, respectively). The seasonal feeding rate (total number of feedings observed divided by total hours watched during the chick-rearing period) for the mixed species pair (1.24 feeds/hour) was lower than the mean seasonal feeding rate of six conspecific Roseate pairs that were feeding only one chick (1.63 ± 0.15 feeds/hour), but was still within the range of seasonal feeding rates for these six pairs (1.24–2.30 feeds/hour). Furthermore, the chick initially grew as quickly as Roseate chicks in the same subcolony, but after nine days its growth rate slowed such that it weighed less than all Roseate chicks under study, and after 15 days its weight actually dropped by 18% (Fig. 3).

On the morning of 19 July (17 days after hatch) both the Roseate and Arctic terns landed with fish near the nest site three to four times, walked around the nest and then flew off, carrying the fish. The chick was not in its regular hiding place that afternoon and I assume it had been taken by a gull. I searched the nest area for the chick's body to ensure it had not starved. The Arctic and Roseate were seen posturing to each other the next day but they brought no fish to the nest.

DISCUSSION

This is the first well-documented case of hybridization between Roseate and Arctic terns. My observations of mate-feeding and copulation as well as the intermediate appearance of the chick (Table 2, Fig. 2) make me confident that hybridization took place between the individuals I observed. There are several possible explanations for this mating; such as the effects of a skewed sex ratio, misimprinting on heterospecific vocalizations by a chick that later affected its mate choice, or parental inexperience.

There is some evidence that the population of Roseate Terns in northeastern North Amer-

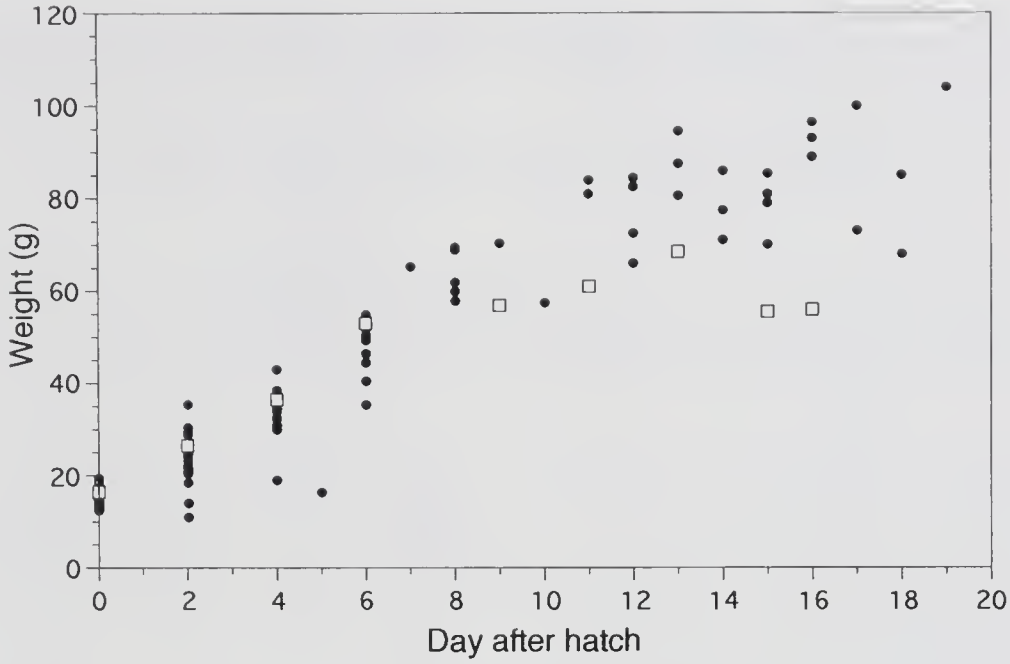

FIG. 3. Growth rate of hybrid Roseate × Arctic chick (□) compared with the growth rates of 30 Roseate chicks (●) on Country Island, Nova Scotia, Canada in 1996.

ica supports an excess of females (e.g., 44.5% males, 55.5% females on Bird Island, Massachusetts; Nisbet 1997). This, combined with an excess of male Common or Arctic terns, could provide favorable conditions for hybridization. When all individuals of the limiting sex are mated, the remainder can hybridize, provided the courtship signals of the two species are similar (Grant and Grant 1997). In fact, in almost every recorded case of hybridization between Roseate and Common terns the Roseate Tern has been female (Ewins 1987, Zingo et al. 1994), providing some support for this hypothesis. Cullen (1956, in Ewins 1987) noted an excess of unmated male Arctic Terns in a colony in Scotland, but nothing is known about the sex ratio of either Arctic or Roseate terns on Country Island.

The mechanics of pair formation may also help explain why interbreeding Roseates are always female (I. C. T. Nisbet, pers. comm.). Terns perform a "high-flight" (Cramp 1985) involving two or more birds that functions as a courtship signal for Roseate, Arctic and Common terns and also as a flying contest for Roseate Terns. Roseates fly much faster than Common or Arctic terns (I. C. T. Nisbet, pers. comm.), such that a female Roseate could keep up with a male Common or Arctic tern, but a female Common or Arctic could not keep up with a male Roseate Tern.

Hays (1975) suggested that Common-Roseate hybrids may arise when young Common Terns are raised by adult Roseate Terns or vice versa. This sometimes occurs when eggs of both species are laid together because of competition for nest sites. Chicks of either species may then learn to recognize and respond to the calls of the species feeding them and later prefer that species when they choose a mate (Hays 1975). Cross-fostered Herring Gull and Lesser Black-backed Gull (*L. fuscus*) chicks later tended to mate with individuals of their foster species (Harris 1970). Grant and Grant (1997) found that song plays a role in the choice of heterospecific mates in Darwin's finches (*Geospiza* spp.), because within hybrid pairs, the song of a female's father was similar to that of her heterospecific mate. Thus, misimprinting on heterospecific calls by chicks of either Roseate or Arctic terns could lead to incorrect mate choice as adults, and could explain why these two birds mated. Unfortunately, I did not record the calls of either the female Roseate or male Arctic tern, which, according to this hypothesis, might have contained similar elements.

Some Common-Roseate hybrid young fledge (Zingo et al. 1994) and may mate with other hybrids to produce F_2 young (Hays 1975). The Arctic-Roseate hybrid survived to 16 days before it was probably taken by a predator. It is impossible to know whether this chick, in the absence of predation, would have

survived to fledge and, eventually, to breed. Its growth rate dropped after both 9 and 15 days (Fig. 3). This decline might be related to either the low rate at which it was fed (i.e., parental inexperience) or to reduced hybrid fitness, but I am unable to separate these possibilities.

Hybridization could be of considerable importance in the conservation of Roseate Terns, which are listed as "Endangered" in the United States and "Threatened" in Canada (U.S. Fish and Wildlife Service 1989, Kirkham and Nettleship 1987). Hybridization with Common or Arctic terns may provide novel gene combinations that could ultimately help individual Roseates adapt to new or changing environments (Grant and Grant 1992). This could be particularly important in populations that suffer from inbreeding depression (Cade 1983). In extreme cases, hybridization can lead to the genetic assimilation of a rare species. For example, the Seychelles Turtle Dove *Streptopelia picturata rostrata* was assimilated by interbreeding with the introduced *S. picturata picturata* from Madagascar (reviewed in Cade 1983). This is unlikely to be a problem for Roseate Terns, however, both because of the apparent infrequency of hybridization and because the Roseate population is still relatively large and widespread.

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BREEDING OF THE WHITE-RUMPED PYGMY FALCON

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ABSTRACT.—A nest of the White-rumped Pygmy Falcon, *Polihierax insignis*, was observed in Thailand for five days during the incubation period. The nest site in a woodpecker hole and the white eggs are described for the first time. Observations on diet, hunting and breeding behavior are also described. The systematic position of the species is discussed. *Received 8 May 1997, accepted 4 Oct. 1997.*

The breeding biology of only one species of pygmy falcon, the African Pygmy Falcon (*Polihierax semitorquatus*), has been studied in any detail (Maclean 1970). We report on five days of observation at a nest of its congener, the White-rumped Pygmy Falcon (*P. insignis*). The six other very small falcons, falconets in the genera *Spiziapteryx* and *Microhierax*, are also relatively little known (Bierregaard 1994, Clark 1994, Kemp and Crowe 1994).

We watched White-rumped Pygmy Falcons near the headquarters of the Huay Kha Khaeng Wildlife Sanctuary, western Thailand, during 28 March to 1 April 1996. A nest of *P. insignis* had been photographed nearby seven years earlier, at about the same time of year (Pilai Poonswad, pers. comm.). Nakhasathien and Stewart-Cox (1990) describe the sanctuary in detail.

METHODS

We discovered an active nest about 1 km south of the headquarters, close to the start of the Khao Hin Dhaeng Nature Trail, at 15° 36′ 10.9″ N, 99° 19′ 1.5″ E and an altitude of 210 m a.s.l. The nest was discovered at 12:50 on 28 March after watching for a pair of pygmy falcons that had been seen copulating in the area several weeks before (Thannyalax Suntaramat, pers. comm.).

The nest area was watched from 12:00 to 19:00 on 28 March (except when erecting a blind at 14:00–15:00), dawn (06:00, local sunrise 06:25) to dusk (19:00, local sunset 18:25) on 29 March, 06:00–12:00 and 14:00–19:00 on 30 March (for photography) and on 31 March, and 06:00–11:00 on 1 April. Three man-days also were spent searching the surrounding area for neighboring pairs, including the use of playback of the distinctive male song. At the end of the study, the nest tree was climbed and the cavity inspected.

Observations were made at the peak of the hot dry season, with daily temperatures exceeding 40° C and only brief drizzle falling from the afternoon build-up of clouds. The pair were quite approachable and observations were made either on foot or from a ground hide of saplings and foliage erected 20 m south of the nest tree. A pair of 10 × 40 binoculars and a 15–60× telescope facilitated observation. Vocalizations were recorded with an ECM-K100 microphone to a Sony WM-D3 cassette recorder and were analyzed with AVISOFT-SONOGRAPH PRO Windows version 2.5 software.

RESULTS

Nest site.—The nest tree was an emergent 24 m-tall *Shorea obtusa* tree with a dbh of about 90 cm, one of several larger trees along the crest of a low ridge in dry deciduous dipterocarp forest. Trees in the forest were about 15–20 m high, with some larger emergents, and the overall impression of the vegetation was a dense 2 m-high scrub layer, with numerous bare tree trunks up to about 10 m, topped by an uneven and partly open canopy. The ridge with the nest tree was about 1 km east of the foothills of the Thanon Thongchai mountains, which run north-south down the Thailand-Myanmar border. The foothills were covered in denser, taller bamboo and evergreen forest.

The nest was in an old woodpecker hole on the north-east side of the trunk, the entrance being 12 m above ground and 2 m below where the first branches emerged. Below and on the same side as the falcon nest, at between 7–10 m, were two old overgrown and four new holes in which three (two males and a female) Greater Flameback (*Chrysocolaptes lucidus*) woodpeckers returned to roost each evening. The tree, which appeared healthy up to the lowest hole, had growths on the trunk

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TABLE 1. Hourly rates in *Polihierax insignis* of prey delivery to the female by the male and of hunting from the nest by the female, during three days of observation within the incubation period.

Sex	Delivery or hunting rates per hour, starting at:													Number of events
	06	07	08	09	10	11	12	13	14	15	16	17	18	
Male	0.7	0.7	1.3	0.7	0.0	0.0	1.0	1.0	0.5	1.3	0.3	0.7	0.0	22
Female	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	3.5	1.3	1.7	0.3	0.0	19
Days observed	3	3	3	3	3	1	2	2	2	3	3	3	3	

above, sparse foliage and a large dead limb above the canopy.

The oval nest entrance was 9 cm high by 8 cm wide and the nest floor was 9 cm below the lower lip of the entrance. The nest cavity, which had a diameter of about 32 cm, was lined with fine wood chips. Overall, the nest hole was similar to the woodpecker roost holes below. On the afternoon of 1 April, the nest contained two plain white, rounded-oval eggs that measured 35.4 × 25.6 mm and 32.5 × 24.7 mm.

Incubation behavior.—The female incubated during the day, although the male sometimes entered the cavity briefly during or after delivering food. The male roosted in the nest with the female, entering at 18:45 on 28 March, leaving again at 06:09 on 29 March and returning to sleep at 18:47 that evening. Both entered the nest at 18:55 on 1 April as soon as the nest inspection was completed.

The female spent most of the time in the nest cavity, only coming to the entrance when hearing the male or other birds nearby (see below). During the heat of the day she also perched at the nest entrance, from which she sometimes pursued nearby prey. Rates of prey delivery and capture (Table 1) indicate that, except for a late morning break, the male provisioned the nest throughout the day and that the female hunted from the nest in the heat of the afternoon.

Hunting behavior and diet.—We never saw the male hunt, despite numerous attempts to follow him as he left the nest area. His small size made it difficult to detect him as he seemed to hunt from low perches or from deep within the foliage. Judging from where he disappeared and then re-appeared with prey, the male appeared to hunt within about 400–600 m of the nest. Prey delivered to the nest by the male included eight lizards, a cicada, an unidentified insect and 12 unidentified items. Most of the lizards appeared to be *Draco* flying lizards (or at least slender agamids with long tails, large hind legs and, in two individuals, expandable throat flaps). Unidentified items were small and were probably insects. The male of a neighboring territory was seen to catch a *Draco* lizard at 13:20 on 1 April, darting 25 m from a perch 3 m up to snatch the lizard from 2 m above the ground off a 6 cm diameter branch of a small tree.

The female confined her hunting to within 50 m of the nest tree, striking either from the nest entrance or from a nearby perch after a previous attempt. Most prey (N = 17) were not identified because they were consumed where captured, usually behind foliage, or were carried rapidly to the nest. A cicada and a grasshopper were identified and probably most prey was of this size, given that consumption time was usually less than a minute and no large prey, such as lizards, was seen being carried to the nest.

We saw the female attempt to capture prey 13 times. Six attempts were to the ground, four into foliage, and three to a branch or twig. Strike distances estimated to the nearest 10 m were 40 m (1), 30 m (1), 20 m (2), 10 m (6) and 0 m (vertical, 1). Four of these strikes, one to the ground among dry leaves and three into foliage (31%), were successful. Two of the successful strikes were upwards from the perch, at the underside of the foliage, and one downwards.

Calls and displays.—The male repeated a shrill flight call *chwirr chur chur* (Fig. 1a), singly or in series, when flying to the nest with food. The female responded with a monotonously repeated and less harsh *cheep* call (Fig. 1b). This call was also used when the male was absent. It appeared to be a food solicitation call since it was often given for long periods when the female perched at the nest entrance and hunted for herself in the after-

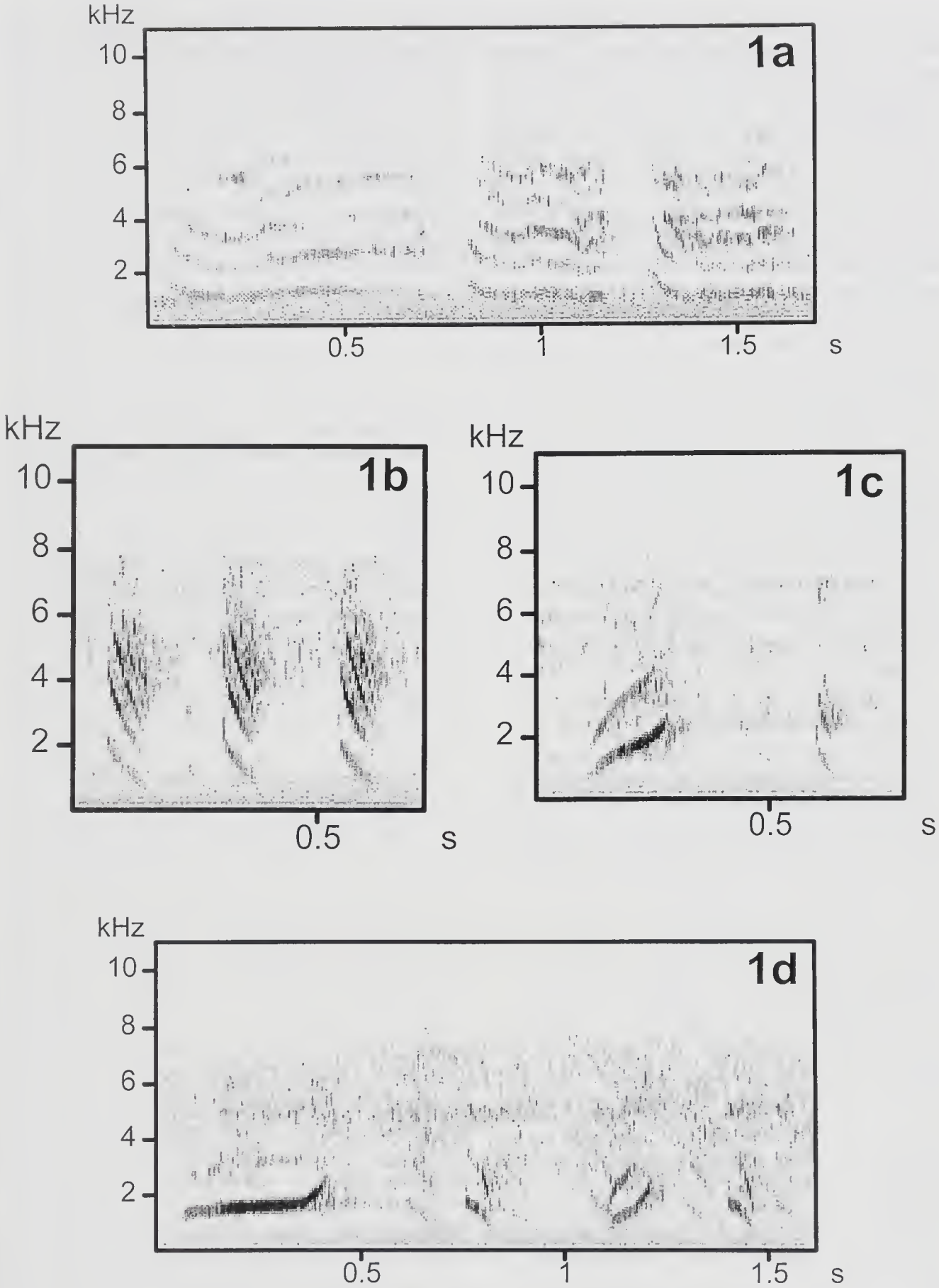

FIG. 1. Sonograms of the main calls of *Polihierax insignis*. Male flight call (1a), female food solicitation call (1b) and male song at low (1c) and high (1d) intensity. See text for further details.

noon. The intensity of the call was a soft purr when the female was alone (Fig. 1b), accelerating to a harsh screech when the female was perched next to the male carrying food. The female sometimes flew calling up to 200 m from the nest to meet the male and solicit prey.

After the flight call, and especially after presenting prey, the male often uttered a short musical song. This was delivered either in abbreviated form as a simple whistle-like phrase *wee-you* (Fig. 1c) or as a more developed series *wee-you-pity-you* (Fig. 1d). The latter somewhat resembles the *twee twee twip* song of the African *P. semitorquatus* (Maclean 1970; sonagram in Maclean 1993). The song was given either in the nest, if prey was presented there, or after returning to a nearby perch. The song was repeated, sometimes several times, especially if the female was out of the nest and perched nearby. The male also uttered a harsh insistent *sheer,* either as a single note in alarm or rapidly repeated if nervous. This was often given as he hung at the nest entrance and once when he was dived at by an Indian Cuckoo (*Cuculus micropterus*) away from the nest area.

The male carried prey in his feet until near the nest and then, at a perch or in flight, transferred it to his bill. This enabled him to land at the nest entrance or on a perch with the food ready to pass to the female. Several times the male refused initially to pass prey to the female. Sometimes he ate some himself and at least twice he eventually consumed the whole lizard without feeding the female. Once the male appeared to threaten the female, mantling with wings drooped and three-quarters open, after which he flew off to eat the prey. Such encounters were noisy, accompanied by loud soliciting (female) and singing or alarm calls (male).

The pair clung at the nest almost like a woodpecker or parrot, braced on their tails, and they were also able to run up the trunk without opening their wings. Twice the male landed lower down on the nest trunk without food and scuttled between the woodpecker roost holes, entering one or other for a brief period and even calling from within. Their antics on the nest trunk or when trying to snatch prey from branches indicated unusual flexibility of their leg and toe joints.

Both birds performed exaggerated head bobbing when examining potential prey. Apart from mantling prey, no other display postures were recorded under natural conditions. However, playback of selected calls were performed once each on the male when he was about 200 m away from the nest. Playback of the male flight call and female solicitation call produced no visible reaction. Playback of the male song caused the male to fly towards the nest, stopping several times en route to sing in reply and once, during an intense period of 6–8 songs, to pump his tail up and down five times through about 45°; the effect, with the wings drooped, was to flash the white rump and display the white-spotted tail.

One evening, at 17:41, the female emerged from the nest to perch with her plumage fluffed. She then preened vigorously before flying east towards a sandy track. After 15 min she returned to the nest without food and when the track was examined later, signs on the sand suggested recent dust bathing. A pair of pygmy falcons had been sketched one evening a few months earlier while dust bathing together on a sandy track just north of the headquarters (Thannyalax Suntaramat, pers. comm.).

Presence of and reaction to neighbors.— No neighboring pairs of pygmy falcons were found by searching. However, on 1 April at 13:20 we were called to see a male in the grounds of the headquarters. We watched it catch a lizard, consume the forequarters and then carry the hindquarters off in a north-easterly direction. Although no nest was located, the behavior suggested a second breeding pair, probably neighbors, with a nest at least 1.5 km north of the study nest.

The falcons at the nest were especially aggressive to a pair of Hill Mynahs (*Gracula religiosa*) that visited the nest tree as many as five times a day. The female always came to the nest entrance when she heard the mynahs call upon landing in the nest tree and once, when she had hunted away from the nest, she dived at the mynahs on her way back to the nest entrance. The female also came to the entrance on hearing a Shikra (*Accipiter badius*) calling overhead, or when Hair-crested Drongos (*Dicrurus hottentottus*), themselves building a nest 50 m away, uttered alarm calls.

At least three pairs of Shikra had nests

within earshot of the falcon nest, the nearest about 400 m away, and the area was also visited several times by Collared Falconets (*Microhierax caerulescens*) and Black Baza (*Aviceda leuphotes*). At least five other species of large woodpeckers also visited the falcon nest area and could have provided alternate nest sites: Common Flameback (*D. javanense*), Greater Yellownape (*Picus flavinucha*), Lesser Yellownape (*P. chlorolophus*), White-bellied Woodpecker (*Dryocopus javensis*) and Black-headed Woodpecker (*P. erythropygius*).

DISCUSSION

Our observations corroborate most aspects of a recent summary of the biology of the White-rumped Pygmy Falcon (Clark 1994). They emphasize the importance of lizards in the diet, especially as large prey items delivered to the nest when breeding. Specialization for hunting on trunks and foliage may explain the limited overall range of this species in dry deciduous forests. Such arboreal and terrestrial hunting differs notably from the more aerial hunting above the canopy of sympatric *Microhierax* falconets (Kemp and Crowe 1994).

However, previous reports of the White-rumped Pygmy Falcon nesting in old stick nests and laying off-white eggs (Swann 1933, Clark 1994) appear erroneous; the white eggs placed in a cavity nest, as described here, are typical of all other Old World falconets.

Phylogenies of the 60 species of Falconidae suggests three phylogenetic and ecological clades: (1) caracaras (polybori, 8 species), (2) forest and laughing falcons (micrasturi, 6 species) and (3) true falcons (falconi, 46 species) [Amadon and Bull 1988, Kemp and Crowe 1990, Griffiths 1994 (who includes the laughing falcon with the true falcons)]. The first two clades are Neotropical in distribution, but the true falcons are cosmopolitan. The true falcons include the three genera and eight species of pygmy falcons and falconets, which are scattered across the Neotropical, Afrotropical and Indomalayan biogeographic realms (Amadon and Bull 1988). Phylogenetically, these dimunutive species represent basal clades to the 38 species of larger falcons and kestrels in the genus *Falco* (Kemp and Crowe 1990, Griffiths 1994).

The two species in the genus *Polihierax* occur on different continents (Africa, Kemp 1994, and Asia, Clark 1994). Both have marked sexual dimorphism, the male with more gray and the female with more rufous markings. Both pump the tail in display, the African species more frequently (Maclean 1970), but so do some true falcons in the Americas and on some Indian Ocean islands (Kemp and Crowe 1994), including the Madagascar Kestrel (*F. newtoni,* Siegfried and Frost 1970). Males of both *Polihierax* species also utter a distinct song of similar structure. *Polihierax insignis* has been separated previously, on tail and primary dimensions, into the genus *Neohierax* (Swann 1922). This separation is supported by a phylogenetic study of syringeal morphology (Griffiths 1994). In a further distinction, the African *P. semitorquatus* nests in cavities within the nest structure of other birds, in the same way as the South American Spot-winged Falconet (*Spiziapteryx circumcinctus;* Bierregaard 1994), while the Asian *P. insignis* is now known to nest in tree holes excavated by other birds, like the five species of Asian *Microhierax* falconets (Clark 1994).

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BREEDING BIOLOGY AND BEHAVIOR OF THE PLUMBEOUS KITE

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ABSTRACT.—We studied Plumbeous Kites (*Ictinia plumbea*) in Tikal National Park, Petén, Guatemala, from 1991–1996. We documented productivity of 19 nesting attempts and studied behavior at six nests each during incubation and nestling periods. Nesting was highly synchronous among pairs, with eggs hatching late in the dry season and young fledging at the onset of the rainy season, a time of maximal prey abundance. Kites built stick nests high in exposed situations in living or dead trees, often reusing the same nest or a nearby alternate site in subsequent years. We observed only clutch sizes of one. Based on museum records, latitudinal variation in clutch size occurs, with single-egg clutches the norm except at the northern- and southernmost limits of the species' range, where two-egg clutches have been found. Fifty-eight percent of eggs hatched, and 64% of those resulted in fledged young, producing 0.37 fledglings per nesting attempt. Pair members shared incubation duties in a 60:40 ratio, and each adult caught its own food throughout the nesting cycle, differing from most raptors in these respects. We hypothesize that these patterns result from prey characteristics that make it inefficient for the male to provision the female at the nest. During incubation, one adult or the other was on the nest 97.8% of the time, and incubation shifts averaged 1.99 h. Two incubation periods were 32 and 33 days, and four nestlings fledged at an average age of 38.5 days. Similar to Mississippi Kites (*Ictinia mississippiensis*) in most regards, Plumbeous Kites laid a smaller clutch, and, unlike Mississippi Kites, held regularly-spaced breeding sites 0.5 km apart and exhibited intraspecific territorial behavior. *Received 17 July 1997, accepted 3 Nov. 1997.*

The Plumbeous Kite (*Ictinia plumbea*) forms a superspecies or is conspecific with the Mississippi Kite (*I. mississippiensis*; Sutton 1944, American Ornithologists' Union 1983, Parker 1988). Plumbeous Kites inhabit humid lowlands from eastern Mexico to Bolivia, Argentina and Paraguay, while Mississippi Kites breed widely across the southern U.S.A. and winter in South America (Brown and Amadon 1968). Migratory at the southern and northern limits of their range, Plumbeous Kites vacate Mexico and Central America to winter in South America (Eisenmann 1963). Breeding biology of the Mississippi Kite is relatively well studied (Skinner 1962; Parker 1974, 1988; Evans 1981; Glinski and Ohmart 1983; Shaw 1985), but that of the Plumbeous Kite is known from only one nest (Skutch 1947). Here we present data collected during a six-year period on the breeding biology and behavior of Plumbeous Kites at a Central American lowland site.

STUDY SITE AND METHODS

We studied Plumbeous Kites in Tikal National Park, Petén, Guatemala from 1991–1996 as part of The Peregrine Fund's "Maya Project." Tikal National Park covers 576 km^2 in NE Guatemala (17° 13′ N, 89° 38′ W). Elevation is 160–450 m amsl, topography gently rolling, and the climate tropical with annual rainfall of about 1350 mm. The rainy season begins between mid-May and late June, and lasts through January, with highest rainfall in September, and a pronounced dry season occurs from February until May or June.

Tikal National Park is covered mostly by unbroken primary forest. Some areas experienced light selective logging prior to 1969, but were practically indistinguishable from primary forest. Vegetation is semideciduous tropical forest, which varies along a subtle topographic continuum; in well-drained sites it is 25–30 m tall with closed canopy, open understory, and diverse tree species, while in low-lying areas it is lower (10–15 m) with more open canopy, dense understory, and differs in tree species composition. Vegetation, climate, and land-use patterns of the Tikal area were described by Lundell (1937), Schulze (1992) and Whitacre and coworkers (1993, 1995). Clearings in the forest existed around Maya ruins and facilities near the park center.

During the incubation period, we studied adult behavior at two 1994 nests and four 1995 nests, for a total of 133 h of observation on 17 days. On 9 days observations were dawn-to-dusk or nearly so (Table 1). During the nestling period we documented prey deliv-

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TABLE 1. Incubation roles of pair members at six Plumbeous Kite nests.

Site/pair	Date	Duration of nest observation session	Percent of time one adult or other was on nest	Percent of time on nest contributed by	
				Bird 1[a]	Bird 2[a]
Mundo Perdido	9 April, 1994	4.12 h	98.4	60.5	39.5
Mundo Perdido	25 April, 1994	6.0	97.8	61.1[b]	38.9[b]
Temple 1	17 April, 1994	12.87	97.4	52.6[c]	47.4[c]
Temple 1	2 April, 1995	12.58	99.5	75.5	24.5
Temple 1	4 April, 1995	10.57	98.0	56.4	43.6
Mundo Perdido	3 April, 1995	11.50	98.4	51.7	48.3
Mundo Perdido	5 April, 1995	12.82	93.8	56.2[d]	43.8[d]
Bajada la Pina	6 April, 1995	10.25	74.8	65.7	34.3
Bajada la Pina	18 April, 1995	12.88	64.8	—	—
Grupo G	21 April, 1995	13.03	99.0	75.8	24.2
Grupo G	24 April, 1995	12.75	85.9	56.2[e]	43.8[e]
Mean		10.85	91.6	61.2	38.8
Median		11.5	97.8	58.45	41.55
SD		3.05	11.7	8.7	8.7

[a] Distinction between Bird 1 and Bird 2 is valid only within each observation session.
[b] Mean of two possible extremes: Bird 1 = 64.05 or 55.11; Bird 2 = 32.95 or 44.89.
[c] Based on 8.58 hours of observation period.
[d] Mean of two possible extremes: Bird 1 = 59.1 or 53.4; Bird 2 = 40.9 or 46.6.
[e] Based on 7.3 hours of observation period.

eries at six nests—two each in 1991, 1992, and 1994. Behavioral data during the nestling period were taken at the two 1992 nests, in mostly day-long observation periods totalling 184 h, and at the two 1994 nests (171 h), where most observations were 2–6 h, distributed throughout the day.

Nests were observed from Mayan temples or the ground, using 30× spotting scope and binoculars at a distance of 15–30 m. Plumbeous Kites were not sufficiently dimorphic for us to distinguish males and females. However, we were able to keep track of individual pair members (designating them as "a" and "b") for long periods. Except to verify some clutch sizes and laying and hatch dates, we avoided climbing to nests until after fledging. To determine clutch sizes, we climbed to nests at least twice, the second time a few days after the first, to verify whether additional eggs had been laid in the interim. In calculating mean heights of nests and nest trees, each was used only once, though some were occupied in multiple years. Values given are mean ± standard deviation except as stated; the median is used where distributions were notably asymmetric.

Statistical tests employed SYSTAT (Wilkinson 1990). To examine the likelihood that the population of nests from which clutch sizes were recorded contained two-egg clutches that were undetected, we conducted Monte Carlo simulations (Crowley 1992) using Resampling Stats software (Simon 1995). We simulated the 43 documented clutches from tropical populations (all of which were 1-egg clutches), testing the probability that this observed sample was taken from a population of nests that in reality included 2-egg clutches in proportions 0.5, 0.3, 0.1, 0.07 and 0.05. In each simulation we conducted 15,000 repetitions in order to estimate probabilities.

RESULTS

Nesting Biology

Migration and nesting phenology.—Plumbeous Kites began nesting in March, soon after their arrival at Tikal in late February–early March (Vásquez et al. 1992; Whitacre et al., unpubl. data). We recorded three laying dates, six hatching dates and seven fledging dates, estimating additional dates based on incubation and nestling intervals (Table 2). The earliest laying date observed was 18 March and the latest fledging date was 11 June. Two incubation periods were 32 and 33 days, and the nestling period was 38.5 ± 1.5 days (n = 4; range = 36–40). Ten pairs laid eggs between 18 March and 5 April (mid-to-late dry season) and six of these did so during the last week of March (Table 2). Eggs hatched in late April and early May (late dry season), and young fledged in late May and early June (onset of rainy season). Plumbeous Kites departed Tikal in August (Vásquez et al. 1992; Whitacre et al., unpubl. data).

Nests and nest sites.—All study nests were associated with forest openings ranging from a narrow dirt roadway to clearings of several

TABLE 2. Breeding phenology of Plumbeous Kites at Tikal, Guatemala.

Territory and year	Egg laid	Egg hatched	Nestling fledged
Airstrip 1992	18 March	20 April	28–29 May
M. Perdido 1996	22-25 March[a]	23–26 April[a]	1–3 June
Bodega 1991	22-23 March[a]	24–25 April[a]	3–4 June
Temple 1 1991	26 March[a]	28 April	na[b]
M. Perdido 1992	27 March	28 April	3 June
M. Perdido 1994	28 March[a]	29 April	7 June
Champon 1996	28 March[a]	29 April[a]	6 June
Airstrip 1991	29 March[a]	30 April	na[b]
Temple 1 1994	1 April[a]	1–3 May	11 June
Champon 1994	5 April	na[c]	na[c]

[a] Estimated dates based on hatching or fledging intervals.
[b] Nest failed during nestling period.
[c] Nest failed during incubation period.

ha. Nests were in live trees isolated from or emerging above surrounding forest, with no or minimal crown contact with neighboring trees. In addition, we noted six nests in open farming landscape near Tikal in similarly isolated trees, three of which were dead. Tree species used for nesting were *Cedrela mexicana* (4 trees used 1, 2, 2 and 3 times), *Bernoulia flammea* (2 trees used 1 and 2 times), *Ceiba pentandra* (4 trees used once each), *Aspidosperma megalocarpon* (1 tree used once) and *Swietenia macrophylla* (1 tree used once). Nest trees were dry season deciduous. Because nest building and incubation took place late in the dry season, the trees were usually leafless making the nests conspicuous. Nests became less conspicuous during the nestling period when nest trees leafed out at the onset of the rainy season.

Nests averaged 25.5 m above ground (SD = 7.1 m, n = 12, range = 13–36 m), while nest trees averaged 30.0 m tall (SD = 7.9, n = 10, range = 17–40 m). Nests were in forks created by two or more limbs, usually against the bole or on major limbs (n = 8), but sometimes in slender limbs toward the outer part of the crown (n = 4). Nests were high and exposed to sun and wind. Three of 12 nests were built on large clumps of bromeliads. Nests were of dry sticks, lined with sprigs of green leaves; both sexes participated in construction. Throughout incubation and nestling periods adults periodically added green sprigs to nests.

Nest spacing, alternate sites and reoccupancy.—Kites nested in the same nests or in other nearby trees from year to year. Alternate nest trees within a given territory were less than 150 m apart. When nesting areas were thoroughly checked in years subsequent to discovery, they rarely lacked a current nesting attempt. Six territories had known occupancy status over 2–4 year periods, totaling 20 territory-years. Birds nested in 18 territory-years, were present but non-nesting in one territory-year, and absent in another. In both the latter instances, they may have nested in an adjacent site. Contiguous, active nests averaged 500 m apart (SD = 52 m, n = 4, range = 453–570 m).

Clutch size.—We documented clutch size for eight nests at Tikal; each had a single egg. Nine other Tikal nests each contained a single nestling. We collated data on 38 *Ictinia plumbea* egg sets, apparently the total holdings of U.S. museums. Most were from Venezuela (19), Brazil (7) and Veracruz, Mexico (7), with one each from Trinidad and El Salvador, and three from Paraguay. All were one-egg clutches except for three from the Tropic of Capricorn near Horqueta, Paraguay, which were two-egg clutches. In addition, published accounts indicate two-egg clutches at the northern extreme of the species' range; Belcher and Smooker (1934) reported a clutch of one and a clutch of two from Trinidad, while Sutton and coworkers (1950) observed a nest with two nestlings in Tamaulipas, Mexico. All other primary accounts we examined mentioned only single-egg clutches and broods of one (e.g., Dickey and van Rossem 1938, Thurber et al. 1987).

Parker (1988) concluded that most 1-egg clutches in Mississippi Kites resulted from

loss of an egg from a 2-egg clutch. Using Monte Carlo simulations, we found that the probability of drawing 43 single-egg clutches from a population of nests comprised partly of 2-egg clutches is as follows for specific assumed frequencies of 2-egg clutches in the population. For 50% and 30% 2-egg clutches in the population, $P < 0.001$; for 10% 2-egg clutches, $P < 0.012$, for 7% 2-egg clutches, $P < 0.05$, and for 5% 2-egg clutches, $P > 0.05$. Hence, it is unlikely that the underlying population of nests contained as many as 7% 2-egg clutches at the time they were documented. We conclude that, except at the northern- and southern-most extremes of the species' range, the modal clutch size of Plumbeous Kites is a single egg.

Reproductive success.—We documented the fate of 19 nestings in which eggs were laid. Eight nests failed during incubation, while 11 hatched a single egg each. Four of the latter nests failed during the nestling period, and seven nests fledged a single young each. Assuming that the 11 nests where laying was inferred from behavior received single-egg clutches, 11 of 19 eggs (58%) hatched, 7 of 11 young (64%) fledged, and 7 of 19 eggs/nests (37%) produced a fledgling, for a productivity of 0.37 fledglings per nest and 1.00 per successful nest. Two nestlings fell from nests during windstorms, and two were believed killed by predators.

Behavior of Adults

Incubation period.—During the incubation period, one adult or the other was on the nest nearly constantly (median = 97.8% of the time; n = 11 observation days at 6 nests; Table 1). When no kite was on the nest, adults remained vigilant, with one usually perched in or near the nest tree or soaring nearby. Both sexes incubated, switching roles periodically throughout the day. On average, one adult provided 61% of incubation and the other 39% (SD = 8.7%, n = 11 observation days at six nests; Table 1). Pair members caught their own prey throughout the incubation phase; we witnessed only two prey exchanges between adults (cicada-sized insects) during 133 h of nest observation.

Periods on the nest averaged 1.99 h (SD = 1.31, n = 24, range = 0.17–4.93). Switches appeared to be initiated by the arriving bird, which typically perched in the nest tree or nearby, occasionally calling as it approached or landed. The incubating bird then stepped off the nest, walked up a limb a short way, and flew off as the arriving bird hopped to a perch near the nest and walked down the limb to settle on the nest. At 5 of 30 switches observed, the arriving bird brought material to add to the nest.

While on the nest, adults alternated between incubating and standing in the nest cup—preening, stretching, rolling or shading the egg. Egg shading (standing over the egg with wings drooped and partly spread) occurred mainly during periods of direct sunlight. Incubation bouts averaged 15 min (SD = 13; n = 100), and standing bouts averaged 3 min (SD = 3; n = 99; range = 1–10). During the mid-day hours, incubation bouts were interrupted more frequently by bouts of standing in the nest, mostly shading the egg. As a result, incubation bouts were significantly longer prior to 09:00 CST (21.6 ± 3.7 min, n = 15, P = 0.002; Tukey HSD test) and marginally longer after 14:00 (17.5 ± 3.7 min, n = 15, P = 0.078; Tukey HSD test), than during mid-day (09:00–14:00; 11.1 ± 0.9 min, n = 67). Duration of standing bouts did not differ significantly with time of day (ANOVA; F = 1.85, n = 98, $P > 0.05$), although the briefest intervals (1 min) occurred mostly in early morning and late evening.

Nestling period.—Hatchlings were covered with white down and had dark eyes, yellow cere, and black bill. Most aspects of behavior were as described by Skutch (1947). In flight, adults carried prey in the bill or feet, but transferred it to the bill before landing near the nest. The adult would often lift the prey in its foot and, using its bill, feed small pieces to the nestling.

An adult arriving with prey either fed the nestling directly or transferred the item to the brooding adult, who then fed the nestling. Such transfers between adults were common while nestlings were newly-hatched, and decreased significantly in incidence thereafter (Fig. 1; F = 12.9, n = 49, $P < 0.001$ in ANOVA comparing weeks). Week one differed from all other weeks (df = 43; $P < 0.001$; Tukey HSD test). This pattern indicated that a shift of parental roles occurred during this period, with one pair member performing

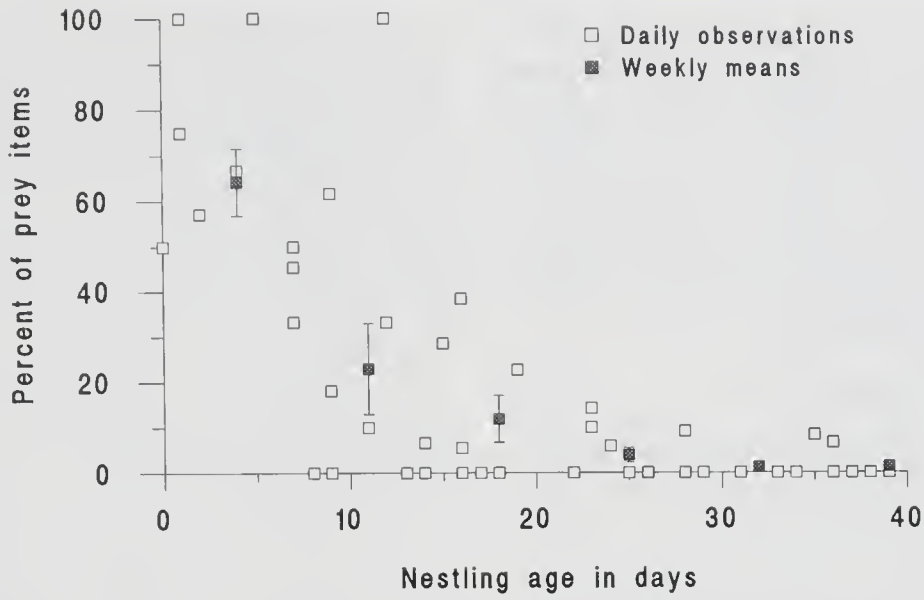

FIG. 1. Percent of prey items transferred to adult at nest before being fed to nestling, versus nestling age, at four Plumbeous Kite nests. Each data point represents one daily observation period. Mean ± SE is given for each week since hatching, for four nests.

most brooding and feeding while nestlings were newly-hatched, and pair members sharing these tasks more evenly as nestlings grew older. Throughout the nestling period each adult captured its own food.

Overall, prey were delivered to nests at the rate of 1.75 ± 1.64 items per hour (n = 49 observation periods; range = 0.25–11 items/h). Prey delivery rates did not differ significantly with nestling age (F = 1.69, n = 49, $P > 0.05$ in ANOVA comparing weeks since hatching). However, the six highest delivery rates (3.7–11.0 prey/h) were noted between nestling ages 16 and 32 days, and all occurred during sessions when prey was never transferred between adults at the nest, that is, when both adults appeared to be bringing prey. During the week prior to fledging, instances of both adults being away from the nest vicinity, presumably hunting, were more frequent.

Interspecific interactions.—During the incubation phase, defense of the nesting area was confined to the nest tree and occurred most often when potential avian predators approached within a few meters of the nest. During the nestling period, however, kites were aggressive toward certain bird species within a 100–200 m radius of the nest. Typically the kite voiced a loud, two-note call as it chased or swooped repeatedly at the interloper. Species most commonly eliciting such a reaction were the Roadside Hawk (*Buteo magnirostris*), Bat Falcon (*Falco rufigularis*), and American Swallow-tailed Kite (*Elanoides forficatus*). Keel-billed Toucans (*Ramphastos sulfuratus*) and Brown Jays (*Cyanocorax morio*) were also chased when in the nest tree or immediate vicinity. Black Vultures (*Coragyps atratus*) and Short-tailed Hawks (*Buteo brachyurus*) were chased once each. In contrast, parrots were commonly in the nest tree but rarely chased. Plumbeous Kites and Bat Falcons chased one another, especially in a case where the two nested less than 100 m apart.

Plumbeous Kites were often harassed by songbirds including Sulphur-bellied Flycatchers (*Myiodynastes luteiventris*), Melodious Blackbirds (*Dives dives*), Social Flycatchers (*Myiozetetes similis*) and Brown Jays. Intense mobbing sometimes turned back a kite approaching the nest with prey, and songbirds sometimes struck a kite or clung to its back momentarily. We saw no evidence of Plumbeous Kites depredating bird nests.

Agonistic behavior.—We observed seven interactions among Plumbeous Kites involving more than the mated pair; two of these appeared territorial while the others suggested a subdued form of territoriality. In one interaction a kite left the nest vicinity to make an aggressive tail-chase at a conspecific that had approached the nest tree. In another case, a nesting kite flew from the nest tree toward a conspecific perched within 100 m. It flushed the perched bird, and remained perched in that

tree as the interloper withdrew. In the remaining five cases when Plumbeous Kites other than the mate approached a nest tree, one or both of the nesting birds flew to meet the approaching kite(s) and then followed behind at a constant distance of 10–15 m, until the conspecific was out of sight of the nest (often >1 km). The nesting kites appeared to escort rather than pursue the interlopers.

DISCUSSION

Plumbeous Kites at Tikal were notably synchronous in nesting phenology, with 7 of 10 laying dates falling within the last week of March and 5 of 7 birds fledging during the first week of June. These kites, which were largely insectivorous at Tikal, fledged at the onset of the rainy season, a time of maximal insect abundance (Seavy et al. 1997). Such reproductive phenology conforms to a pattern prevalent among insectivorous birds in Central America (Skutch 1950).

Nests were positioned high in open-canopied trees, making them accessible to kites without entering the forest canopy, and visible, perhaps facilitating defense by adults perched or soaring nearby. Nest trees were isolated from or emergent over the forest canopy, which may reduce nest predation by climbing predators.

One of our most noteworthy results was the relatively even sharing of incubation duties by pair members (a 60:40 ratio of incubation effort), with each pair member providing its own food needs during this period. A similar pattern was noted in Mississippi Kites (Parker 1988), with males only occasionally delivering prey to incubating females (Glinski and Ohmart 1983). This is in marked contrast to the majority of raptor species, in which females conduct most incubation and males are often sole providers for female and nestlings until the latter are partly grown (Newton 1986). The pattern shown by Plumbeous Kites, with pair members sharing about equally in incubation, and foraging for themselves during this time, does occur, however, in the *Gyps* vultures (Houston 1976, Newton 1979), in all three U.S.-breeding cathartids (Jackson 1998a, b; Snyder 1988), and in some small, largely insectivorous falcons, e.g., the Lesser Kestrel (*Falco naumanni*) and Western Red-footed Falcon (*F. vespertinus*; Cade 1982).

We propose that this near-equal sharing of incubation duties, with each pair member capturing its own food, results from the small size of prey taken by Plumbeous Kites. It would not be energetically efficient for the male to provision the female at the nest with such small items. Furthermore, we hypothesize that any factor that makes it energetically more efficient for each pair member to forage than for one to provision the other at the nest will promote evolution of shared incubation and self-feeding during incubation. Predisposing factors should include not only a diet of small prey, but also reliance on prey that are sparsely and patchily distributed, ephemeral, or of unpredictable occurrence in time and space. These characteristics of prey place a premium on the ability of individual adults to remain away from the nest for substantial periods, and to consume prey where it is found rather than carrying it to an incubating mate. These descriptors apply to large animal carrion—the principal food of vultures—and to many concentrations of airborne insects, e.g., mating swarms of ants, termites, mayflies, and others (Whitacre 1992).

The hypothesis outlined above is supported by a study of American Swallow-tailed Kites (Snyder 1974), whose aerial hunting and diet resemble those of the Plumbeous Kite. In American Swallow-tailed Kites, males performed about 36% of incubation (Snyder 1974), similar to our results for Plumbeous Kites. In a year when hylid frogs (a predominant prey item) were abundant, males fed females during incubation about once every 2.5 h, but in a year when kites subsisted mainly on insects, such feedings were rare (2 in 85 h), and the female studied that year provided essentially all of her own food during incubation (Snyder 1974).

The incubation intervals we documented (32 and 33 days) were similar to the 29–32 day period reported for the Mississippi Kite (Parker 1988). Our inference that one parent assumed primary brooding responsibilities while nestlings were young also parallels the Mississippi Kite, for which Evans (1981) reported that females with nestlings 10 days old spent twice as much time at nests as did males. Despite this pattern of females apparently spending more time than males in nest attendance during the first 2–3 weeks of the

nestling period, females continued to meet nearly all of their own food demands by hunting while males brooded nestlings. Though highest prey delivery rates occurred on days when it appeared both adults were bringing prey to the nest, the occurrence of such high rates was sporadic, and delivery rates were no higher during the week prior to fledging than during the first two weeks after hatching.

Plumbeous Kites at Tikal consistently nested about 500 m apart, with pairs utilizing the same nest trees or nearby alternates repeatedly over a 6-yr period. This regular, substantial spacing, along with our observations of intraspecific aggression, suggest that territorial behavior influenced nesting dispersion and density at Tikal. Dispersion of Plumbeous Kite nests differed greatly from that of American Swallow-tailed Kites, which are similar in diet, hunting style, and choice of nest site. The area occupied by our Mundo Perdido and Temple 1 Plumbeous Kite territories often supported up to 12 nests of American Swallow-tailed Kites, some as close together as 35 m (R. Gerhardt, pers. comm.). Nests of the latter species were grouped into loose colonies, while extensive areas of forest had few or no nests (pers. obs.).

The social organization we observed in Plumbeous Kites falls at one end of a spectrum displayed by the Plumbeous/Mississippi Kite superspecies. Mississippi Kites show a clear tendency toward colonial nesting in the Great Plains (Parker 1988), where kites often aggregate nests in a single shelterbelt, leaving similar nearby sites unoccupied, and where colonies sometimes relocate en masse to other shelterbelts. Within shelterbelts, density approached 1 nest/ha, with most nests less than 100 m apart, and once as close as 13 m (Parker 1988). The tendency toward colonial nesting is apparently somewhat reduced in areas of extensive woodland in the eastern U.S. and in expanses of oak savannah and mesquite, where kites tend to nest farther apart (Parker 1988, pers. comm.), but published literature does not present clear evidence of regular and substantial internest spacing like that we observed at Tikal.

In light of the variable social organization of the superspecies, it is interesting to consider the subdued agonistic interactions we observed. Parker (1988, pers. comm.) stated that intraspecific territorial defense is unknown in the Mississippi Kite. In Plumbeous Kites at Tikal, we observed intraspecific aggression, but it was not strong. We speculate that the degree of tolerance toward conspecifics near the nest is facultative in this superspecies, and varies depending on conditions, which sometimes favor gregarious nesting, and other times favor dispersed nesting. Though much Plumbeous Kite hunting occurred within 200 m of the nest, much also occurred farther afield (Seavy et al. 1997). The extent to which the prey base of Plumbeous Kites is economically defensible is uncertain. Cicadas, beetles and lizards comprised at least 45% of the diet at Tikal (Seavy et al. 1997). These seem uniformly distributed throughout the forest, and hence may represent a defensible prey resource. In contrast, ephemeral aggregations of dragonflies and other flying insects probably are not defensible, but formed only 10% of the identified diet at Tikal. In the Great Plains, the clumped distribution of Mississippi Kite nesting habitat amidst large expanses of foraging habitat may result in high intruder pressure near the nest and in a spatial separation of nest and foraging sites. Together these may inhibit the development of all-purpose territories and high inter-nest distances. In comparison, the more homogeneous distribution of prey and potential nest sites in areas of extensive forest such as Tikal may permit the expression of a tendency toward wide inter-nest spacing and defense of nest and foraging areas.

Mississippi Kites in the Great Plains, Arizona, and Illinois respectively showed productivity of 0.60, 0.61, and 0.63 young fledged per nest, and 1.00, 1.29, and 1.29 per successful nest (Evans 1981, Glinski and Ohmart 1983, Parker 1988). In comparison, Plumbeous Kites at Tikal had lower productivity, fledging only 0.37 young per nesting attempt, though the number of young fledged per successful nest (1.00) was similar.

In Mississippi Kites, the modal clutch size is two, with clutches of three being very rare and probably in error, and single-egg clutches occasional and also largely artifactual (Sutton 1939; Parker 1974, 1988). In contrast, throughout most of its range, the only clutch size documented for the Plumbeous Kite is one, with two-egg clutches known from the

northern and southern extremes of the species' range. Parker (1974, 1988) found that the frequency of 1-egg clutches in Mississippi Kites reached nearly 50% in some years, and presented evidence that most or all of these resulted from partial loss of clutches. It is possible that some partial clutch loss is represented in the museum and field data reported here for Plumbeous Kites. However, Monte Carlo simulations showed that it is unlikely that a high frequency of 2-egg clutches existed in the population from which the 43 single-egg clutches reported here were taken. We conclude that the modal clutch size of Plumbeous Kites in tropical regions is a single egg, but only further data can verify whether 2-egg clutches occur in tropical populations of this species. The difference in clutch size noted here between Plumbeous and Mississippi Kites, as well as the latitudinal variation in clutch size documented for the Plumbeous Kite, fit the latitudinal gradient in clutch size well-known for many birds (Moreau 1944).

In summary, the breeding biology and behavior of the Plumbeous Kite at Tikal bear strong resemblance to those of the Mississippi Kite. The smaller clutch size and greater manifestation of regular nest-spacing and territorial behavior in the Plumbeous Kite are the greatest differences in nesting biology of these two species now known.

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THE BEGGING BEHAVIOR OF NESTLING EASTERN SCREECH-OWLS

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ABSTRACT.—The behavior of adults and nestlings at nine Eastern Screech-owl (*Otus asio*) nests in central Kentucky was monitored by videotaping the owls in specially-constructed nest boxes. Adult screech-owls delivered 1281 prey items during 164 h of taping. Nestlings fed first by adults started to beg significantly earlier, extended their beaks higher and closer to the adult, and called at higher rates and with greater volume than did siblings that were not fed first. In addition, nestlings fed first started begging earlier, stretched their beaks higher, positioned their beaks closer to the adult, and vocalized at a higher rate than when they were not fed first. In addition, after being returned to the nest, nestling screech-owls temporarily deprived of food begged with greater intensity and were fed more often than siblings. Such results provide further evidence for the positive relationship between hunger, begging intensity, and the chances of being fed. Our results also indicate, however, that nestling mass may be important in determining which nestlings will be fed when differences in the mass of siblings reach a certain level. We observed no siblicide or other aggression between siblings. Contributing to this absence of aggression may have been the large boxes used for videotaping and an abundant food supply. It is also possible, however, that aggression and siblicide occur infrequently in broods of screech-owls. *Received 28 Dec. 1996, accepted 29 July 1997.*

Evidence is accumulating that parental provisioning behavior can be influenced by nestling behavior (Stamps et al. 1985, 1989; Wright and Cuthill 1989; Teather 1992). Altricial nestlings may improve their chances of being fed by seeking a particular position in the nest, reaching higher and closer to the visiting adult, and vocalizing first or with the greatest intensity (e.g., Smith and Montgomerie 1991, Teather 1992). Such behavior may be correlated with hunger level. For example, Smith and Montgomerie (1991) experimentally prevented parents from feeding nestling American Robins (*Turdus migratorius*) and found that both the intensity of begging and the number of feedings subsequently received by food-deprived nestlings increased.

Begging intensity may not be the only factor that determines which nestling will be fed by adults; size may also play a role. For example, small Yellow-headed Blackbird (*Xanthocephalus xanthocepthalus*) nestlings beg more than larger siblings but are fed less (Price and Ydenberg 1995). Similar results have been reported in other species where siblings differ in size as a result of asynchronous hatching (e.g., Ryden and Bengtsson 1980).

Among raptors and other species where nestlings possess "weapons" (beak and talons), access to food delivered by parents also can be influenced by direct interactions among siblings. For example, Allen (1924:4–5) observed three nestling Eastern Screech-Owls (*Otus asio*) competing for access to a prey item (a bird) and reported that "after one such tug-of-war . . . two of the young attacked the third and picked most of his bones by morning."

With the exception of Allen's (1924) limited observations, little is known about the behavior of nestling Eastern Screech-Owls and, specifically, how nestlings gain access to the food delivered by parents. The objective of our study was to examine the begging behavior of nestling screech-owls and, more precisely, to determine the importance of begging behavior and nestling size in the distribution of food to nestlings by adult screech-owls.

Eastern Screech-Owls are socially and genetically monogamous (Lawless et al. 1997). Both adults feed nestlings and the most common prey delivered to nestling screech-owls in central Kentucky include beetles, crickets, and beetle larvae (Hofstetter 1995). Adults typically feed nestlings at the cavity (or nestbox) entrance and one nestling is usually fed per visit (Hofstetter 1995). The nestling period averages about 28 days (Gehlbach 1994, pers. obs.).

STUDY AREA AND METHODS

We conducted this study at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison County, Kentucky. During March and April 1994, we checked nest boxes and

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natural cavities for incubating or brooding female screech-owls. Once located, nests (n = 9) were monitored until nestlings were 11–14 days old. Nestlings and the adult female at each nest were then transferred into nest boxes designed for video-taping. These video-taping boxes were placed in the same location as, or immediately adjacent to, the nest cavity or nest box.

Video-taping boxes had a chamber (20 × 31 × 41 cm) for the owls and a larger one for a cameorder. The smaller chamber was equipped with two small fluorescent lights to permit taping at night. The cameorder was set at a 25–30° downward angle from the horizontal to permit video-taping of both the nestlings and the visiting adult.

At the time of transfer, each owlet was banded with a U.S. Fish and Wildlife Service numbered aluminum leg band and uniquely color-marked on the top of the head using colored "Sharpie" markers. We also collected 200–400 μl of blood from each nestling for use in another study (Lawless et al. 1997).

Video-taping generally began the day after owls were transferred to the video-taping boxes and continued until the young owls fledged. Video-taping sessions were 2–4 h in duration, with each tape lasting 2 h. All taping occurred during the period from just prior to sunset (about 20:30) until 01:30.

All video-tapes were subsequently viewed and analyzed using a Sony video recorder/player (Model SLV-701HF) and a 19 inch color television. During analysis of the tapes, we quantified the begging behavior of nestlings and determined how parents allocated food among nestlings. The begging intensity of individual nestlings was ranked in a manner similar to that described by Smith and Montgomerie (1991). For each visit by a parent to the nest, each nestling was ranked based on several behaviors, including: (1) when the nestling started to vocalize after the parent's arrival (start rank), (2) the height to which each nestling extended its bill (height rank), (3) the distance of the nestling's bill from the parent (position rank), (4) the vocalizing rate (rate rank), and (5) the volume (or intensity) of vocalizations (volume rank). Height and distance ranks were estimated at the instant a parent arrived at the nest box entrance. The vocalizing rate was determined by counting the number of calls (with a call defined as any continuous sound) during the period between the parent's arrival and the feeding of a nestling. The relative volume of each nestling's calls during the period between a parent's arrival and the feeding of a nestling was estimated and ranked. For each parental visit, therefore, each nestling's relative begging intensity was determined using its rank scores.

Because brood size varied from 2–5, ranks were not comparable between nests. Therefore, as suggested by Smith and Montgomerie (1991), ranks of begging intensity were standardized to [(rank − 1)/(brood size − 1)], where 1 is the lowest and 5 the highest rank. Standardized ranks, therefore, varied from 0 to 1, with a lower standardized rank indicating more intense begging.

Nestlings were weighed every other day. To examine the possible effects of nestling mass on the behavior of nestlings and adults, nestlings were categorized as "small," "medium" and "large" in broods where the difference between the mean mass of the lightest and heaviest nestlings was at least 9 g (n = 19 nestlings from six broods). The mean difference in mass of large and small nestlings at these six nests was 21.5 g (range = 9.2–51 g). Small nestlings (n = 8) had a mean mass of 99.7 ± 3.4 g, medium nestlings (n = 3) 107.8 ± 3.3 g, and large nestlings (n = 8) 115.5 ± 2.8 g. These differences in mass were significant ($F_{2,21}$ = 15.3, P < 0.001).

To determine the effect of nestling hunger level on the begging behavior of nestlings, randomly-selected nestlings (one from each of four nests) were temporarily removed from their nest boxes and, thus, were not fed for 2 h. These nestlings were returned to their nest box, positioned randomly with respect to the entrance and their siblings, and the nest was then video-taped for at least two additional hours. These tapes were then analyzed in the manner described previously.

Wilcoxon rank sum tests (SAS Institute 1989) were used to compare the ranks of (1) nestlings fed first versus siblings not fed, and (2) nestlings fed first versus the ranks of the same nestlings when not fed. Ranks of small, medium, and large nestlings were compared using repeated measures analysis of variance (SAS Institute 1989). Likelihood ratio χ^2 tests were used to determine if nestlings (either experimental versus non-experimental nestlings or small, medium, and large nestlings) were fed in a non-random manner. Statistical analyses were performed using the Statistical Analysis System (SAS Institute 1989). All values are presented as mean ± one standard error.

RESULTS

Nine screech-owl nests were videotaped on 33 nights for a total of 164 h. Each nest was taped for an average of 18.2 ± 4.2 h (range = 8–32 h). Adult screech-owls delivered 1281 prey items, with an average of 142.3 ± 52.5 prey items delivered per nest (range = 36–404 prey items). Adults always delivered one prey item per visit and typically fed just one nestling per visit (98.1% of all visits). Adult screech-owls (male and female combined) delivered prey to nestlings an average of 8.80 ± 0.97 times per hour.

Nestling begging behavior.—To determine if the begging intensity of the first nestling to receive food during a parental visit differed from that of its siblings, we compared the ranks of the nestling fed first with the average rank of its siblings. Using one randomly-chosen nestling from each nest, we also compared the mean ranks of nestlings when fed first to the ranks of that same nestling when not fed

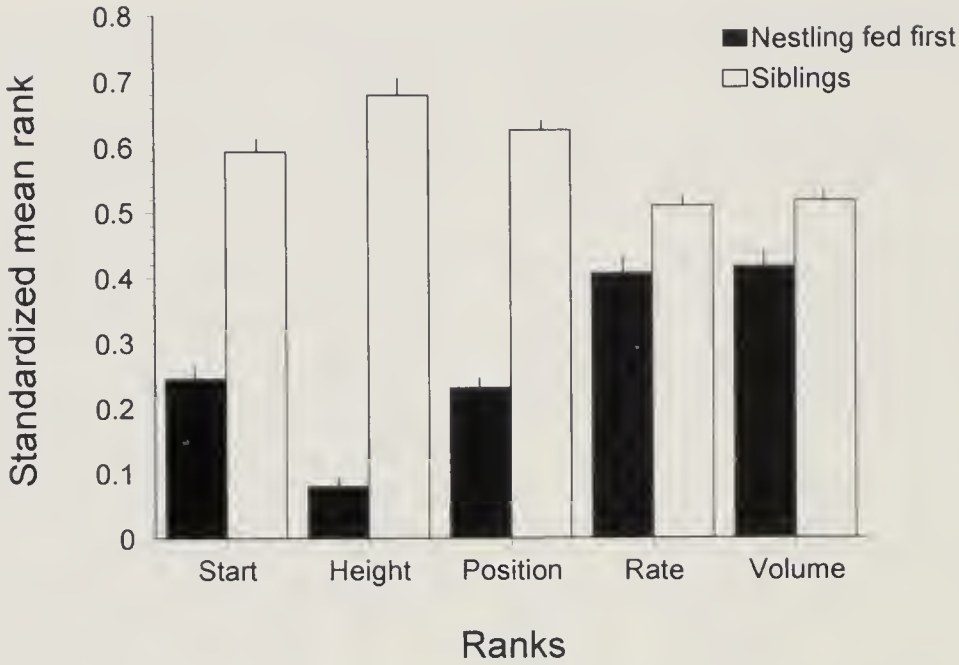

FIG. 1. Standardized mean ranks of nestling screech-owls fed first and those of siblings not fed first. See text for definition of terms.

first. Nestlings that were fed first started to beg significantly earlier (z = 25.1, P = 0.001), extended their beak significantly higher (z = 41.4, P = 0.001), and held their beaks significantly closer to the adult (z = 28.4, P = 0.001) than siblings that were not fed (Fig. 1). Nestlings fed first also gave significantly louder calls (z = 6.5, P = 0.001) at a significantly greater rate (z = 6.6, P = 0.001) than nestlings that were not fed (Fig. 1).

The rankings for randomly chosen nestlings (one from each of the nine nests) when fed first were also compared to their rankings when not fed (Fig. 2). Nestlings fed first started begging significantly earlier (z = 13.3, P = 0.001), stretched their beaks significantly higher (z = 25.2, P = 0.001), positioned their beaks significantly closer to the adult (z = 15.1, P = 0.001), and vocalized at a significantly higher rate (z = 3.0, P = 0.0031) than

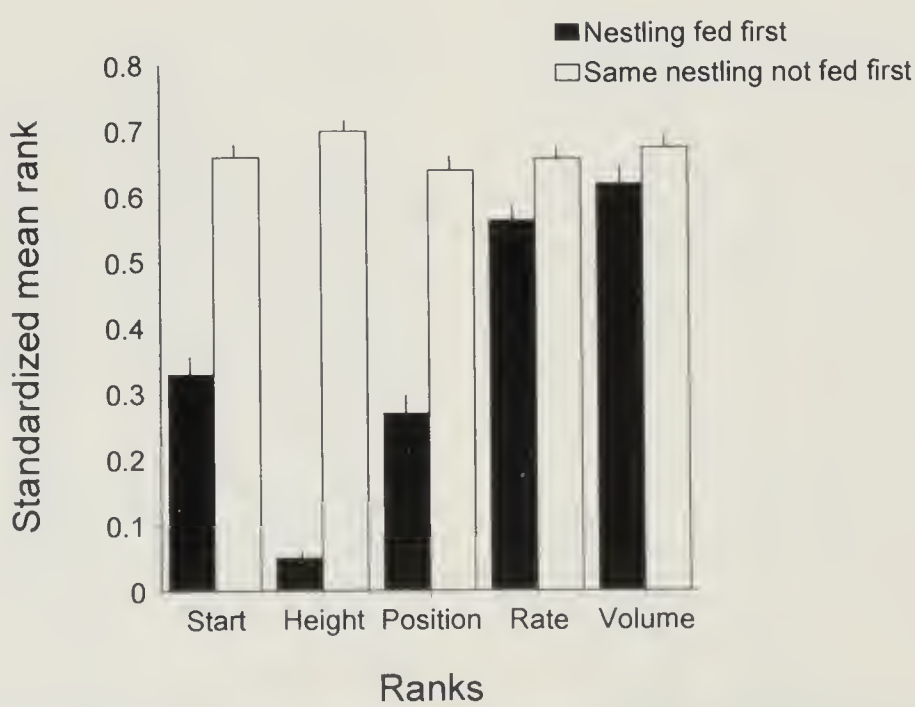

FIG. 2. Standardized mean ranks of individual nestling screech-owls when fed first and of the same nestling when not fed first.

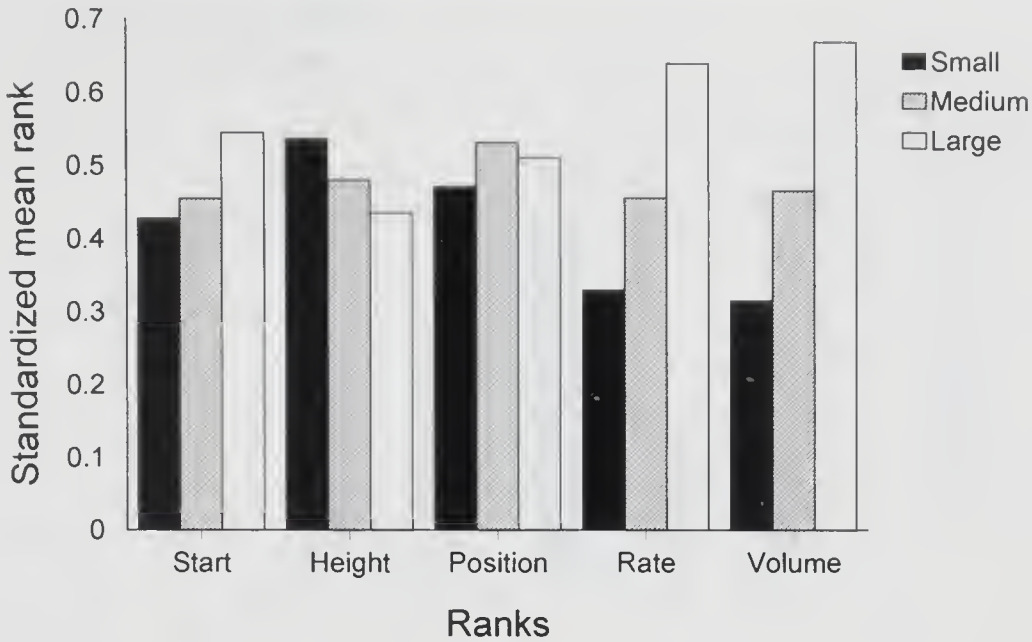

FIG. 3. Standardized mean ranks of small, medium, and large nestling screech-owls.

when not fed. However, nestlings fed first did not call with greater volume (z = 1.5, P > 0.05) than when not fed.

Nestling mass.—For all six nests in which young were categorized by mass, the standardized mean ranks of small, medium, and large nestlings did not differ significantly (repeated measures ANOVA, P > 0.05; Fig. 3). Analysis of individual nests revealed significant differences in mean standardized ranks of siblings at only one nest (Nest 8; Wilcoxon tests, P < 0.001). Two nestlings were present at this nest and these nestlings differed substantially in mean mass (108 g versus 57 g). Comparison of these two nestlings indicates that, upon arrival of an adult with food, the smaller one generally started begging earlier, was positioned closer, and called with greater volume and at a greater rate (Fig. 4). However, the larger nestling almost always extended its beak higher (Fig. 4).

Overall, the distribution of feedings among small, medium, and large nestlings was significantly non-random (χ^2 = 22.7, df = 2, P < 0.001; N = 6 nests), with adults feeding large nestlings more frequently than expected

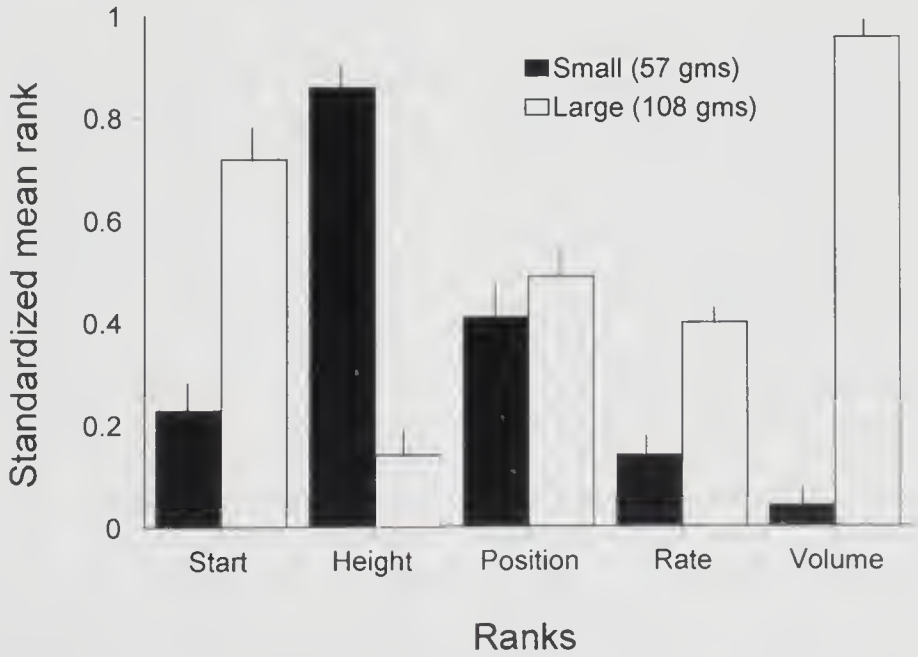

FIG. 4. Standardized mean ranks for the small and large nestlings at Nest 8.

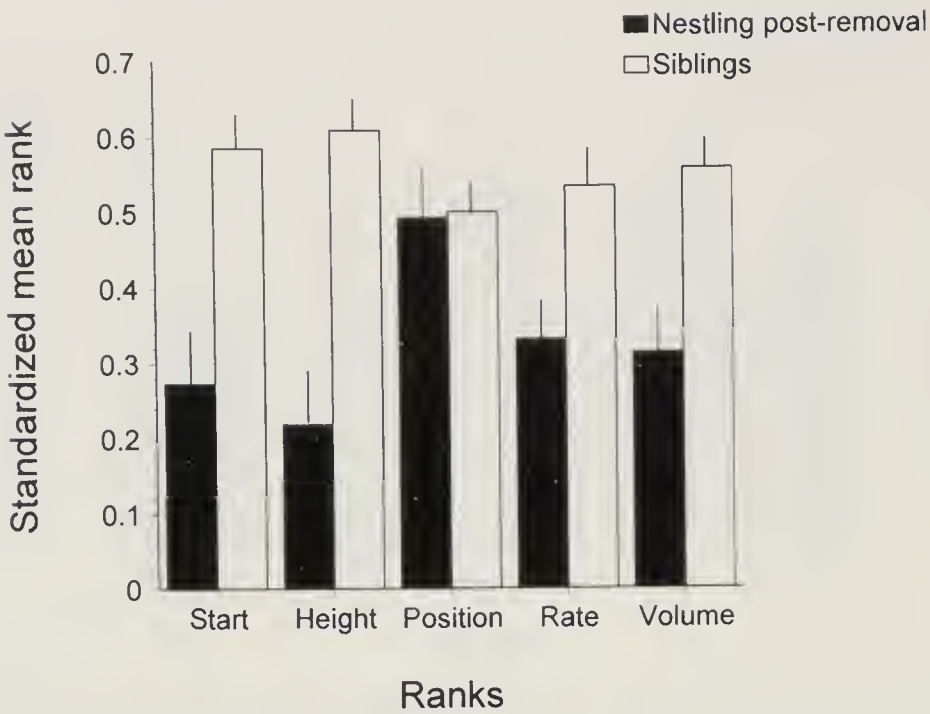

FIG. 5. Standardized mean ranks of temporarily-removed nestling screech-owls (food deprived) and those of siblings that were not removed (not food deprived).

and small nestlings less frequently than expected. Examination of individual broods revealed, however, that differences in the distribution of feedings among nestlings was significantly non-random only at Nest 8. Of 145 prey items delivered by adults, the large nestling obtained 117 (80.7%) (χ^2 = 117.4, df = 1, $P < 0.001$).

For the remaining five nests, small, medium, and large nestlings were fed a similar number of times (χ^2 = 0.7, df = 2, $P > 0.05$). The difference in mean mass of the smallest and largest nestlings at these five nests was 9.2, 12, 14, 15.5, and 27.5 g, respectively.

Nestling removal.—Nestlings prevented from eating for a 2 h period begged with significantly greater intensity than their siblings after being returned to the nest (Fig. 5). Four of five begging indices were significantly lower for such food-deprived nestlings than for their siblings (start rank, height rank, volume rank, and rate rank; Wilcoxon tests, $P < 0.027$). The position rank of food-deprived nestlings did not vary from that of siblings (z = 0.1, $P > 0.05$).

Food-deprived nestlings (N = 4) were fed more often (χ^2 = 13.6, df = 1, $P < 0.001$) than siblings (N = 10) during the 2 h period after being returned to the nest. Food-deprived siblings (N = 4) received 55.2% of all prey delivered to their nests during that period.

Nestling aggression and mortality.—Previous investigators have reported facultative siblicide by nestling Eastern Screech-Owls (Allen 1924, Gehlbach 1994). During 164 h of observation, however, we saw no direct aggression (grabbing with talons or biting) among siblings either during or between feedings.

One nestling apparently died shortly after being transferred to a video-taping box. This nestling, noticeably smaller than its two siblings, disappeared within 24 h after transfer so we had not yet started videotaping. At the time of transfer we noticed no injuries or wounds. It is likely that this nestling died of starvation and, because no remains were found, its carcass was probably cannibalized.

DISCUSSION

Adult screech-owls were more likely to feed a nestling that started begging earlier, extended its beak higher and closer to the visiting adult, and called at a greater rate and with greater volume than did its siblings. In addition, after being returned to the nest, nestling screech-owls deprived of food begged with greater intensity and were fed more frequently than siblings (who were fed by parents in the absence of their sibling). Such results agree with the findings of other investigators (Smith and Montgomerie 1991, Redon-

do and Castro 1992, Price and Ydenberg 1995) and provide further evidence for the positive relationship between hunger, begging intensity, and the chances of being fed.

Our results also indicate that nestling size or mass may be important in determining which nestling will be fed by adults. At one nest with two young (Nest 8), the smaller nestling consistently begged with greater intensity than the larger nestling but the larger nestling still obtained 80.7% of the prey delivered by adults. Observations of this nest in conjunction with those at the other nests reveal two features of screech-owl begging behavior. First, the ability of a nestling to extend its bill higher than siblings appears to be the most important factor in determining which nestling screech-owl will obtain food from an adult. At Nest 8, the smaller nestling consistently started begging earlier, positioned itself closer to the adult, and uttered louder vocalizations at a higher rate than its larger sibling. Despite such behavior, the larger nestling reached higher and received most of the food. Given that screech-owls typically nest in natural cavities and that adults entering a cavity with food would typically approach nestlings from above, reaching higher than siblings would appear to be the best strategy for a nestling screech-owl seeking to obtain food. Second, differences in the size or mass of siblings apparently must be above some minimum value before influencing the distribution of food. At five nests where differences in the mass of smallest and largest nestlings ranged from 9.2–27.5 g (or where the mass of the smallest nestling ranged from 78.4–92.1% of the mass of the largest nestling), nestling mass had no apparent effect on the chances of a nestling obtaining food. Only at the nest where the difference was 51 g (and the mass of the smallest nestling was 52.8% of the mass of the larger nestling) did nestling mass influence the distribution of food. Thus, our results indicate that size may begin to influence the distribution of food to nestling Eastern Screech-Owls when the mass of the smallest nestling is somewhere between 52.8 and 78.4% that of its largest sibling.

Our results indicate that small nestling screech-owls may beg more vigorously than larger siblings (particularly vocally) yet receive less food. Similar observations have been reported in other species that exhibit asynchronous hatching and, therefore, size asymmetries among nestlings (Bengtsson and Ryden 1981, Drummond et al. 1986, Price and Ydenberg 1995). Although calling rate and volume appear to be less important than other behaviors (e.g., beak height) in determining which nestling screech-owl receives food, nestling vocal behavior may influence parental foraging behavior. For example, Bengtsson and Ryden (1983) found that adult Great Tits (*Parus major*) increased feeding rates during periods when recorded calls were played during feeding visits to the nest. Thus, the higher calling rates of small nestling screech-owls may improve their chances of getting some food by increasing the number of feeding visits by adults.

We observed no overt aggression between siblings. In contrast, Allen (1924) observed one case of siblicide. In addition, although no direct observations were made, Gehlbach (1994:116) reported that small nestlings sometimes disappeared from nests during their first 15 days post-hatching and suggested that they "suffered probable fratricide (siblicide) or infanticide and invariable cannibalism . . ." Gehlbach (1994) further suggested that some nestling screech-owls die from starvation and suffocation. One possible reason why we observed no aggression is that our videotaping boxes were relatively large and, as a result, nestlings were not "crowded." Gehlbach (1994) found that greater "brood crowdedness" (more nestlings relative to the size of a cavity or nest box) increased the likelihood of nestling mortality (and, perhaps, the likelihood of siblicide). Another possible reason why we observed no aggression between siblings is that adults provided nestlings with sufficient food. Previous studies suggest that additional food may diminish nestling mortality in facultatively siblicidal species (Mock et al. 1987, Magrath 1989). Finally, it is possible that siblicidal behavior is simply uncommon in Eastern Screech-Owls and that starvation and suffocation are the primary causes of mortality among nestlings.

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INFLUENCE OF CAVITY AVAILABILITY ON RED-COCKADED WOODPECKER GROUP SIZE

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ABSTRACT.—The availability of cavities can determine whether territories are occupied by Red-cockaded Woodpeckers (*Picoides borealis*). However, there is no information on whether the number of cavities can influence group size and population stability. We compared group size between 1993 and 1995 in 33 occupied cluster sites that were provisioned with artificial cavities. The number of groups with breeding pairs increased from 22 (67.7%) in 1993 to 28 (93.3%) in 1995. Most breeding males remained in the natural cavities that they had excavated and occupied prior to cavity provisioning in the cluster while breeding females and helpers used artificial cavities extensively. Active cluster sites provisioned with artificial cavities had larger social groups in 1995 ($\bar{x}$ = 2.70, SD = 1.42) than in 1993 ($\bar{x}$ = 2.00, SD = 0.94; $Z = -2.97$, $P = 0.003$). The number of suitable cavities per cluster was positively correlated with the number of birds per cluster ($r_s = 0.42$, $P = 0.016$). The number of inserts per cluster was positively correlated with the change in group size between 1993 and 1995 ($r_s = 0.49$, $P = 0.004$). Our observations indicate that three or four suitable cavities should be maintained per cluster to stabilize and/or increase Red-cockaded Woodpecker populations. *Received 3 March 1997, accepted 27 Oct. 1997.*

The Red-cockaded Woodpecker (*Picoides borealis*) is an endangered species endemic to the pine forests of the southeastern United States (Jackson 1971). Red-cockaded Woodpeckers are unique among woodpeckers in the use of living pines for cavity excavation (Ligon 1970). The abundance and distribution of suitable cavities and residual pines for cavity excavation play a critical role in Red-cockaded Woodpecker population dynamics (Walters et al. 1992). Red-cockaded Woodpeckers are cooperative breeders, occuring in groups comprised of a breeding pair and 0–3 helpers (Lennartz et al. 1987, Walters et al. 1988). Each group inhabits and defends an aggregate of cavity trees, known as a cluster site, and associated foraging habitat (Hooper 1980, 1982). Group size may be an important factor influencing reproductive success (Lennartz et al. 1987) and population stability (Walters et al. 1988). Management practices which would stabilize and/or increase group size would promote recovery of the species. Artificial cavity techniques developed by Copeyon (1990) and Allen (1991) have provided managers with short-term management tools to offset the limitations of young, second-growth pine forests which typically lack adequate numbers of old-growth trees for cavity excavation. Artificial cavities have been used extensively to supplement Red-cockaded Woodpecker cluster sites having insufficient numbers of suitable natural cavities and to rehabilitate abandoned cluster sites. Such cavity provisioning has been used to stabilize and/or increase populations (Copeyon et al. 1991, Conner et al. 1995, Walters et al. 1992, Gaines et al. 1995, Richardson and Stockie 1995, Watson et al. 1995). Copeyon and coworkers (1991) demonstrated that the availability of cavities can determine whether or not territories are occupied. However, no published information has demonstrated whether the number of cavities can influence group size or population stability.

During surveys conducted between 1987 and 1992, biologists documented the limited availability of suitable cavities in occupied cluster sites on Fort Polk, Louisiana. Red-cockaded Woodpeckers excavate cavities in pines with decayed heartwood (Hooper et al. 1991a). The frequency of such decay is a function of tree age (Hooper et al. 1991a, Conner et al. 1994). Forests on the fort are relatively young (<80 years) and lack large numbers of old trees for cavity excavation. An intensive program was begun in 1993 to install artificial cavity inserts in all active cluster sites on the installation. Here, we describe the effect of cavity provisioning on group size.

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STUDY AREA AND METHODS

The study area was the Fort Polk military installation in Vernon Parish, Louisiana. The installation is currently used for training light infantry and simulating low to mid-intensity conflicts. The population in 1993 contained 33 active Red-cockaded Woodpecker clusters and has since been increasing. It is considered a subpopulation of the adjacent population on the Vernon Ranger District managed by the U.S. Forest Service. Vegetation consists primarily of a longleaf pine (*Pinus palustris*) overstory and an understory of bluestem grasses (*Andropogon* spp. and *Schizachrium* spp.). The area is managed for timber production on an 120-year rotation and prescribed burning is conducted on a 3-year rotation.

Starting in March 1993, artificial cavities were installed in 32 of 33 active cluster sites with fewer than four suitable cavities. Installation was completed by March 1995. Cavities were installed using the insert technique (Allen 1991) at heights of 4.0 m or 7.5 m, depending on the diameter of the trees available in the site. Provisioned cluster sites received up to four inserts depending on the number of usuable excavated cavities that were available in a site. Management of active sites was consistent for all sites during the period that sites were provisioned with inserts. Provisioning was considered a treatment while other variables that may influence population numbers were considered constant during the project. No sites were considered to have significant midstory development and none required midstory removal. All sites selected had adequate foraging according to guidelines of the U.S. Fish and Wildlife Service (1989). However, U.S. Army management guidelines required all suitable sites be provisioned with inserts. The resulting lack of control sites for comparison limits interpretation of our results.

Cavity trees were routinely monitored for activity (Jackson 1978a). All birds were captured on Fort Polk during the fall and winter of 1993 and 1995 as part of a monitoring program initiated in 1993. Birds were banded with unique combinations of colored leg bands and a U.S. Fish and Wildlife Service band. Nestlings have also been banded in the same manner since 1993. Banding birds enabled us to follow individuals as they moved between sites and to monitor changes in group size between years.

Total numbers and mean numbers per cluster of natural and artificial cavities was computed for 1993 and 1995 to assess cavity availability. Unenlarged natural cavities with entrance tunnels approximately 7 cm in diameter were considered useable (Rudolph et al. 1990) and were included in the analysis. Mean group size and mean numbers of helpers were compared between 1993 and 1995 in occupied clusters provisioned with inserts using a Wilcoxon pair-wise test. To assess the relationship between cavity availability and group size, adult group size was compared to the number of available cavities in 1995 and changes in adult group size were compared to the number of inserts installed per site using Spearman rank correlations. A χ^2-test was used to assess differences in the numbers of birds by social status using artificial and natural cavities during 1995. Numbers of birds using artificial and natural cavities during 1995 were used as observed values for the test. Analyses were performed with SPSS Version 6.0 (Norusis and SPSS Inc. 1993).

RESULTS

Thirty of the 33 clusters that were active in 1993 and which were provisioned with inserts were still active in 1995. Almost all (96 of 105) the birds recaptured in 1995 had been banded on the fort in 1993. Of the 105 birds captured in 1995, four birds originated from the population on the Vernon Ranger District. The origin of 5 unbanded birds was unknown. The small number of birds from the Veron population suggests that increases in group size on the fort were primarily the result of internal population changes rather than immigration from the Vernon population. The lack of population data prior to 1993 required our comparison of group size to use data from 1993 when 55 inserts had already been installed. The number of groups with breeding pairs increased from 22 (67.7%) in 1993 to 28 (93.3%) in 1995. By 1995, the number of available cavities had been increased by 139.4% in active clusters as a result of insert provisioning. The total number of inserts available and number of active inserts in 1995 exceeded the total number of natural cavities available and number of active natural cavities, respectively in a site (Table 1). In 1995, inserts comprised 57.9% of all active cavities with 55.6% of inserts being active and natural cavities made up 42.1% of all active cavities with 56.3% of natural cavities being active. The number of natural cavities remained almost constant between 1993 and 1995; only one new natural cavity was constructed during this time. No natural or artificial cavities were lost between 1993 and 1995. Most breeding males remained in the natural cavities which they had excavated and occupied prior to the insert program while breeding females and helpers used inserts extensively (Table 2).

Active cluster sites provisioned with artificial cavities had larger social groups in 1995 ($\bar{x}$ = 2.70, SD = 1.42) than in 1993 ($\bar{x}$ = 2.00, SD = 0.94; $Z = -2.97$, $P = 0.003$). The number of groups with helpers increased from 9 (27.3%) in 1993 to 15 (50.0%) in 1995. Provisioned sites had more helpers in 1995 ($\bar{x}$ =

TABLE 1. Total numbers and mean numbers (± SD) per cluster of natural and artificial cavities available in 1993 and 1995 on Ft. Polk.

	1993		1995	
	Total	No. active	Total	No. active
Total natural cavities	70	54	71	40
Total inserts	55	24	99	55
Mean cavities/cluster	3.79 (1.63)	2.36 (1.11)	5.09 (1.26)	2.76 (1.48)
Mean natural cavities/cluster	2.12 (1.14)	1.64 (0.82)	2.15 (1.12)	1.21 (0.99)
Mean inserts/cluster	1.67 (1.45)	0.73 (0.80)	3.00 (1.25)	1.67 (1.22)

0.70, SD = 0.88) than in 1993 ($\bar{x}$ = 0.33, SD = 0.60; $Z = -1.96$, $P = 0.05$). The number of suitable cavities per cluster was positively correlated with the number of birds per cluster ($r_s = 0.42$, $P = 0.016$; Fig. 1). The number of inserts per cluster was positively correlated with the change in group size between 1993 and 1995 ($r_s = 0.49$, $P = 0.004$; Fig. 2).

DISCUSSION

In 1993, most groups on Fort Polk appeared to be either single males or breeding pairs lacking helpers. The increase in group sizes observed in 1995 resulted from unpaired males acquiring mates and groups retaining males as helpers. The increase in reproduction resulting from additional breeding units should increase the number of subadult birds in the population. Most subadult females disperse and fill breeding vacancies while subadult males may remain as helpers in their natal cluster or disperse (Walters et al. 1988).

Helpers may enhance reproduction within clusters (Lennartz et al. 1987, Walters 1990, Heppell et al. 1994). The critical-resource model proposed by Walters (1990) suggests that cavities are the critical determinant of habitat quality. The addition of cavities to a site with few suitable cavities may enhance the quality of the site by providing additional roosting opportunities and encourage subadult males to remain and potentially inherit the territory. Subadult males which remain in their natal clusters may help stabilize populations by buffering against clusters going inactive as a result of the death of the breeding male. In addition, many solitary males occupying sites in 1993 that we provisioned had secured mates by 1995, suggesting that dispersing females may also prefer sites with many roosting alternatives.

Females, and to a lesser extent helpers, appear to benefit when additional cavities are provided. Females are typically the most subordinate member of Red-cockaded Woodpecker social groups (Walters et al. 1988) and as a result may not always be able to secure an adequate roost cavity. Hooper and Lennartz (1983) observed breeding males, breeding females and helpers roosting in the open or in surplus cavities in adjacent territories when cavities were unavailable in their own site. Individuals roosting in the open may be more vulnerable to predation and/or extreme weather conditions, although no information is available on how much such factors contribute to mortality. A combination of these factors may have contributed to the lower numbers of breeding units and helpers observed in 1993 relative to 1995.

An increase in group size was observed only when at least 3 inserts were installed in a site. Sites with less than 3 inserts had at least 2 inactive, but suitable, natural cavities. The stable or decreasing group sizes in clusters with less than 3 inserts suggests that the remaining inactive natural cavities may not have been suitable for occupation. In addition, most excess natural cavities we considered suitable were not used between 1993 and 1995. Such cavities may have been occupied on a regular

TABLE 2. Numbers of Red-cockaded Woodpeckers by social status using natural and artificial cavities during 1995.

	Number of birds by cavity type			
Status	Natural	Artificial	χ^2	P
Breeding male	23	7	8.53	0.004
Breeding female	8	20	5.14	0.023
Helper	8	15	2.13	0.144

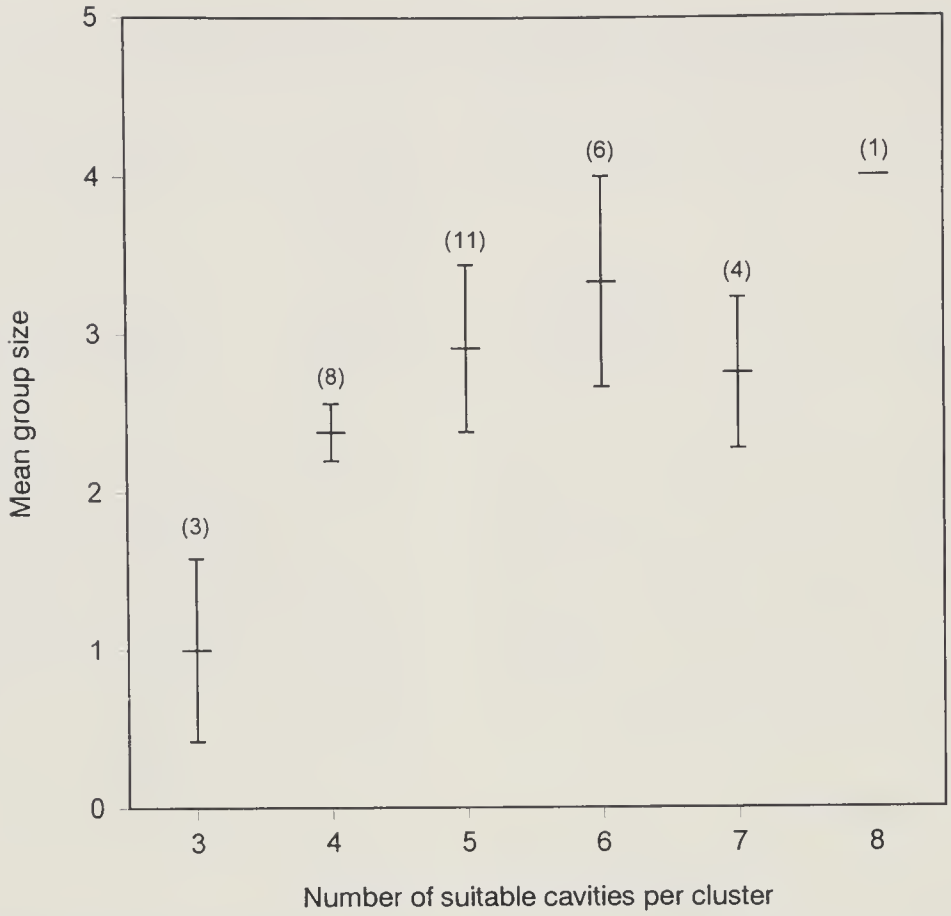

FIG. 1. Relationship between mean group size and number of suitable cavities per cluster in 1995 (bars indicate standard errors; number of clusters in parenthesis).

basis by southern flying squirrels (*Glaucomys volans*), particularly since flying squirrels prefer unenlarged cavities (Rudolph et al. 1990). There is little information on the other factors that may influence the ability of a cavity to remain suitable for Red-cockaded Woodpeckers over time. Birds have abandoned cavities in which the interior chamber had decayed and become too enlarged and deep to remain functional as roost sites (R. Conner, pers. comm.). Cavities we observed with large amounts of dead wood in the plate region surrounding the entrance were seldom used. Dead wood does not produce resin in the area of the plate and may deter use by woodpeckers which normally maintain extensive resin wells around the edges of the plate. The potentially subtle nature of factors influencing cavity suitability requires that the condition and number of surplus natural cavities should be examined closely when determining the number of artificial cavities necessary to supplement or rehabilitate a site.

Surplus cavities in a site may also reduce negative interactions between Red-cockaded Woodpeckers and other cavity-dependent species. At least 24 species of birds and mammals have been identified using Red-cockaded Woodpecker cavities as roost and/or nest sites (Jackson 1974, 1978b; Baker 1971; Harlow and Lennartz 1983; Rudolph et al. 1990). Several instances of interspecific aggression involving cavities have also been documented (Ligon 1971, Baker 1971, Jackson 1978b, Harlow and Lennartz 1983). Such interactions may be intense in clusters with few excess cavities, particularly following the breeding season when juvenile birds begin using cavities. Southern flying squirrels have been proposed as an important kleptoparasite of Red-cockaded Woodpecker cavities (Gaines et al. 1995, Richardson and Stockie 1995). Laves (1996) found an increase in Red-cockaded Woodpecker reproduction and in the number of helpers in treatment groups that had flying squirrels removed. However, Conner et al. (1996) observed no relationship between woodpecker reproductive success and flying squirrel use of cavities and no instances of woodpeckers forced to roost in the open be-

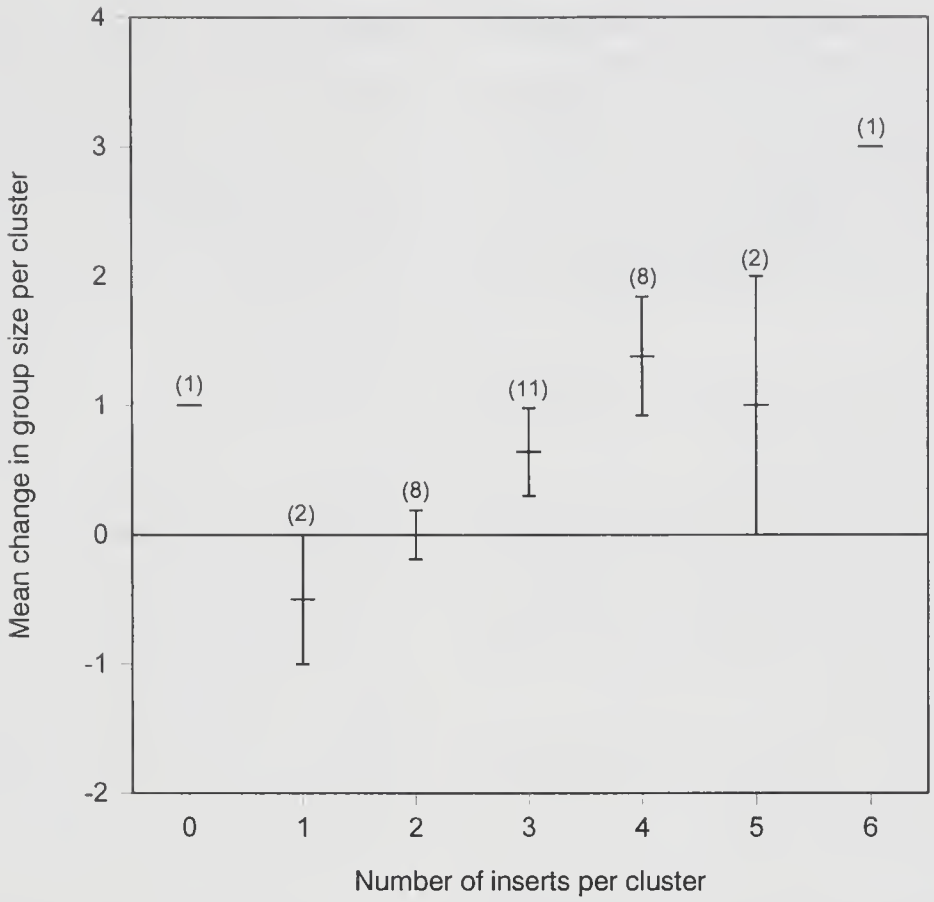

FIG. 2. Relationship between the mean change in group size between 1993 and 1995 and the number of inserts installed per cluster (bars indicate standard errors; number of clusters in parenthesis).

cause of squirrel-caused shortages of unenlarged cavities. Flying squirrels have been frequently found using active Red-cockaded Woodpecker cavities on the fort. Birds that were evicted from their cavities normally roosted in surplus cavities in their cluster or roosted in the open.

Interactions between Red-cockaded Woodpeckers and other cavity-dependent species may be exacerbated in small, declining woodpecker populations that are also stressed by other factors such as isolation and forest fragmentation (Conner and Rudolph 1989, Conner and Rudolph 1991). Negative interactions may be minimized by ensuring that excess cavities are available in each cluster. Because our analysis lacked control sites for comparison, our results may not be definitive and cannot determine an optimum number of suitable cavities. Watson et al. (1995) determined that the population on the Francis Marion National Forest had 3.7 usuable cavities per cluster prior to Hurricane Hugo. At that level, that population was increasing (Hooper et al. 1991b). Our observations and those on the Francis Marion population indicate 3 or 4 suitable cavities should be maintained to stabilize and/or increase Red-cockaded Woodpecker populations.

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SOUTHERN PINE BEETLE-INDUCED MORTALITY OF PINES WITH NATURAL AND ARTIFICIAL RED-COCKADED WOODPECKER CAVITIES IN TEXAS

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ABSTRACT.—Southern pine beetle (*Dendroctonus frontalis*) infestation is the major cause of mortality for Red-cockaded Woodpecker (*Picoides borealis*) cavity trees in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines. Recent intensive management for Red-cockaded Woodpeckers includes the use of artificial cavity inserts. Between 1991 and 1996 we examined southern pine beetle infestation rates of pines with natural vs artificial cavities in loblolly and shortleaf pine habitat on the northern portion of the Angelina National Forest. No significant difference existed in the rate at which southern pine beetles infested and killed pines with natural cavities vs those with artificial cavity inserts ($\chi^2 = 0.84$, $P > 0.05$). Southern pine beetles infested and killed 20 natural cavity trees (25.6%) during the 5-year study (78 cavity-tree years) and 19 artificial cavity trees (18.8%; 101 cavity-tree years). Data for the entire Angelina National Forest indicate that 40% (25 of 62) of the cavity trees killed by southern pine beetles between 1984 and 1996 had been the nest tree during the preceding breeding season. The annual infestation rate of cavity trees appears to be related to southern pine beetle population levels of the surrounding forest. Use of artificial cavities is essential to maintain sufficient numbers of usable cavities for Red-cockaded Woodpeckers in Texas. Why southern pine beetles appear to preferentially infest active Red-cockaded Woodpecker cavity trees is still unknown, but may be related to southern pine beetle attraction to resin volatiles produced when woodpeckers excavate resin wells and/or changes in the levels of infestation-inhibiting tree volatiles as a result of cavity and resin well excavation. *Received 8 April 1997, accepted 23 Sept. 1997.*

Cavity trees are a critical resource for Red-cockaded Woodpeckers (*Picoides borealis*) (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988, 1992). They are essential for reproduction and roosting, require a long period of time to excavate (Conner and Rudolph 1995a), and are often limited in availability (Conner and Rudolph 1989, Costa and Escano 1989, Walters et al. 1992). During the past decade, several studies attributed severe Red-cockaded Woodpecker population declines to several factors, among which was limited availability of cavity trees (Conner and Rudolph 1989, Costa and Escano 1989). Cavity tree mortality, which may further reduce cavity tree availability, may be of great importance for management and recovery of Red-cockaded Woodpecker populations.

The development and use of artificial Red-cockaded Woodpecker cavities to reduce shortages of cavities and facilitate population expansion through the formation of new woodpecker groups has greatly enhanced the forest manager's ability to recover dwindling populations (Copeyon 1990, Copeyon et al. 1991, Allen 1991). Use of artificial cavities has contributed to Red-cockaded Woodpecker population increases in Texas (Conner et al. 1995), Mississippi (Richardson and Stockie 1995), North Carolina and Georgia (Carter et al. 1995), and South Carolina (Gaines et al. 1995, Watson et al. 1995).

The major cause of Red-cockaded Woodpecker cavity tree mortality in loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines is pine bark beetle infestation (Conner et al. 1991, Ross et al. 1995). Of 26 Red-cockaded Woodpecker populations on U.S. Forest Service lands, 19 are primarily associated with loblolly or shortleaf pine habitat (Costa and Escano 1989). Thus, pine bark beetle-induced mortality of cavity trees is a significant potential problem throughout the range of the woodpecker. The majority of bark beetle infestations are primarily composed of southern pine beetles (*Dendroctonus frontalis*). Four other pine bark beetles often occur in association with southern pine beetle infestation in

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varying proportions. These include three species of engraver beetles (*Ips avulsus, I. grandicollis,* and *I. calligraphus*) and, occasionally, black turpentine beetles (*Dendroctonus terebrans*). In this paper, we focus on cavity-tree mortality induced primarily by southern pine beetles.

In Texas, artificial cavities, primarily cavity inserts, have been used regularly to provide sufficient cavities for woodpecker groups that have lost active cavity trees to southern pine beetle infestation (Conner et al. 1995, Rudolph and Conner 1995). However, when Red-cockaded Woodpeckers begin to use artificial cavity inserts and peck resin wells, southern pine beetles infest and kill pines containing cavity inserts, apparently finding them as attractive for infestation as natural cavity trees (Conner and Rudolph 1995b).

We compared the beetle infestation rates of pines containing natural Red-cockaded Woodpecker cavities with pines containing artificial cavities over a 5-year period on the Angelina National Forest. We evaluated instances where only a single Red-cockaded Woodpecker cavity tree was infested and killed. Cavity trees can also be infested and killed as the result of the "growth" of an expanding beetle spot (multiple tree infestation; Billings and Varner 1985, Conner et al. 1995b); no cavity tree deaths resulting from beetle spot growth were observed on the Angelina National Forest during our study.

Red-cockaded Woodpeckers create a resin barrier on the pine's bole that serves as a barrier against rat snakes (*Elaphe* spp.; Jackson 1974, Rudolph et al. 1990). The resin system of pine trees serves as their primary defense against southern pine beetles and some pines with superior resin output can survive beetle attack (Lorio 1986). Pines that are able to produce more resin might be preferentially selected by woodpeckers because they would provide better resin barriers against rat snakes and potentially be more resistant to southern pine beetle infestation. Nebeker and coworkers (1992) observed that wound-induced resin flow rate, total resin flow, and viscosity in loblolly pines were genetically controlled. Red-cockaded Woodpeckers may be able to detect the ability of a pine to produce resin when they begin to excavate a cavity start. In contrast, a cavity tree is selected for a cavity insert based on the openness of its bole and a sufficient diameter (38 cm) at the height of installation to physically contain the cavity insert. No consideration is made for the potential resin production of the trees. This suggests that pines with cavity inserts may be more susceptible to mortality following southern pine beetle infestation, since on the average, they might produce less resin than trees selected by woodpeckers. We hypothesized that pines selected by biologists for installation of cavity inserts were more likely to be infested by southern pine beetles than pines selected by woodpeckers for natural cavity excavation.

We also compared the number of Red-cockaded Woodpecker cavity trees killed by southern pine beetle infestation per year (only single tree infestations, not cavity-tree mortality resulting from beetle spot growth) with beetle population levels in forest stands surrounding woodpecker cavity-tree clusters, and determined the number of active cavity trees killed each year by bark-beetle infestation relative to the total number available.

STUDY AREA AND METHODS

We studied southern pine beetle infestation of Red-cockaded Woodpecker cavity trees on the Angelina National Forest (62,423 ha; 31° 15′ N, 94° 15′ W) in eastern Texas. The northern portion of the Angelina National Forest is predominantly covered by loblolly and shortleaf pines, whereas longleaf pine (*Pinus palustris*) is the dominant tree species on the southern portion of the forest in the areas where Red-cockaded Woodpeckers are found (Conner and Rudolph 1989). The loblolly-shortleaf pine habitat where Red-cockaded Woodpecker clusters occur on the northern portion of the Angelina National Forest is located primarily on mesic, shrink-swell clays (Woodtel and LaCerda soil types), which readily support growth of hardwood vegetation (Fuchs 1980, Conner and Rudolph 1995). Varying moisture conditions throughout the year produce the shrink-swell characteristics of the soils, which can strip root hairs off lateral pine roots, increasing stress and pine susceptibility to southern pine beetle infestation (Lorio et al. 1982, Mitchell et al. 1991, Conner and Rudolph 1995). The longleaf pine habitat where Red-cockaded Woodpeckers occur on the southern portion of the Angelina National Forest is located primarily on deep loamy sands (Tehran and Letney soil types) containing materials of volcanic origin (Neitsch 1982). These soils contain very little organic material resulting in a low water holding capacity. High soil temperatures during summer reduce the water holding capacity in these soils, retarding the growth of hardwoods on these sites and stressing pines, but do not usually affect longleaf pine resin pro-

duction or increase the susceptibility of these longleaf pines to southern pine beetle infestation. Historically, southern pine beetle infestation of cavity trees in the longleaf pine habitats of the Angelina National Forest has been minimal (Conner et al. 1991).

We made annual spring visits to all Red-cockaded Woodpecker cavity trees on the Angelina National Forest (1983 through 1996) to evaluate cavity tree status and condition using the indicators described by Jackson (1977, 1978). Cavity tree clusters occupied by woodpeckers were visited several times per year. We determined the occurrence and causes of all cavity tree mortality (Conner et al. 1991, Conner and Rudolph 1995). Cavity trees infested by southern pine beetles typically had numerous white "popcorn-like" pitch tubes of crystallized pine resin around wounds on the bole where individual beetles had chewed through the bark and into the cambium. Dead cavity trees with signs of bark beetle infestation were examined to determine whether lightning strike was also associated with tree death or if the infestation was caused by other species of bark beetles. Cavity-tree mortality caused by lightning, wind action, and fire have been reported previously (Conner et al. 1991, Conner and Rudolph 1995c).

As part of intensive efforts to recover Red-cockaded Woodpecker populations, a program of cavity insert installation (Allen 1991) began on the Angelina National Forest during 1990 (see Conner et al. 1995). A total of 399 cavity inserts was installed on the northern and southern portions of the forest between January 1990 and spring 1996: 57 between early 1990 and spring 1991, 50 between summer 1991 and spring 1992, 59 during 1992–1993, 31 during 1993–1994, 139 during 1994–1995, and 63 during 1995–1996. Cavity inserts were installed primarily within active woodpecker clusters, but also within inactive clusters and recruitment stands near active clusters.

We used χ^2 analysis to compare southern pine beetle infestation rates of artificial and natural cavity trees in 11 active woodpecker clusters on the northern portion of the Angelina National Forest over a 5-year period between October 1991 and May 1996. We also used χ^2 analysis to evaluate the effect of recency of natural cavity completion or artificial insert activation on likelihood of beetle infestation, as well as the likelihood of beetle infestation of active cavity trees used for nesting and roosting.

To compare southern pine beetle population levels with annual losses of cavity trees, we obtained records of the annual number of southern pine beetle infestations (beetle spots) and the number of pines infested on the northern portion of the Angelina National Forest from the USDA Forest Service Pest Management Office in Pineville, Louisiana, and Atlanta, Georgia (SPBIS—Southern Pine Beetle Information System data base). Pearson correlations were calculated to examine relationships between annual, beetle-induced cavity-tree mortality in 11 cavity-tree clusters on the northern portion of the Angelina National Forest and yearly measures of southern pine beetle population levels in the surrounding forest stands.

RESULTS

Southern pine beetle infestation of Red-cockaded Woodpecker cavity trees has occurred regularly in loblolly and shortleaf pines on the Angelina National Forest over the past 14 years, killing 2–40% of the active cavity trees annually (Fig. 1). Bark beetle-induced mortality of active cavity trees increased after the intensity of woodpecker management increased in the early 1990s following the detection of severe population declines and litigation (Conner and Rudolph 1995b, Conner et al. 1995). Since 1983 on the entire Angelina National Forest, 25 of 62 southern pine beetle-killed cavity trees (40%) had been nest trees during the preceding breeding season. Over a 14-year period an average of 23.1% of the active cavity trees were nest trees in a given year [376 active cavity-tree years (number of active cavity trees each year summed over the 14 years) vs 87 nest tree years in loblolly and shortleaf pines on the Angelina National Forest]. The 40% infestation rate of nest trees is significantly greater than what would be expected based on the ratio of active cavity trees to nest trees on the average (40% vs 23%, $\chi^2 = 13.85$, $P = 0.001$).

Between 1990 and 1996, 399 cavity inserts were installed on the Angelina National Forest. Eighty-seven of these artificial cavities were installed in the 11 active woodpecker clusters we examined closely in loblolly and shortleaf pines on the northern portion of the forest. As a result of cavity-tree losses to southern pine beetles and cavity enlargement by Pileated Woodpeckers (*Dryocopus pileatus*; Conner et al. 1991), most active cavity trees used by Red-cockaded Woodpeckers since 1991 have contained artificial cavities (Fig. 2). During 1992 52% of active cavity trees contained artificial cavities, 63% in 1993, 49% in 1994, 56% in 1995, and 61% in 1996, averaging 56.4% over a 5-year period.

Southern pine beetles infested and killed 39 natural and artificial cavity trees in loblolly and shortleaf pines in the 11 active clusters examined between 1991 and 1996. Of the 39 cavity trees killed by beetles between the fall of 1991 and the summer of 1996, 32 were active and 7 were inactive. Eleven of the 32

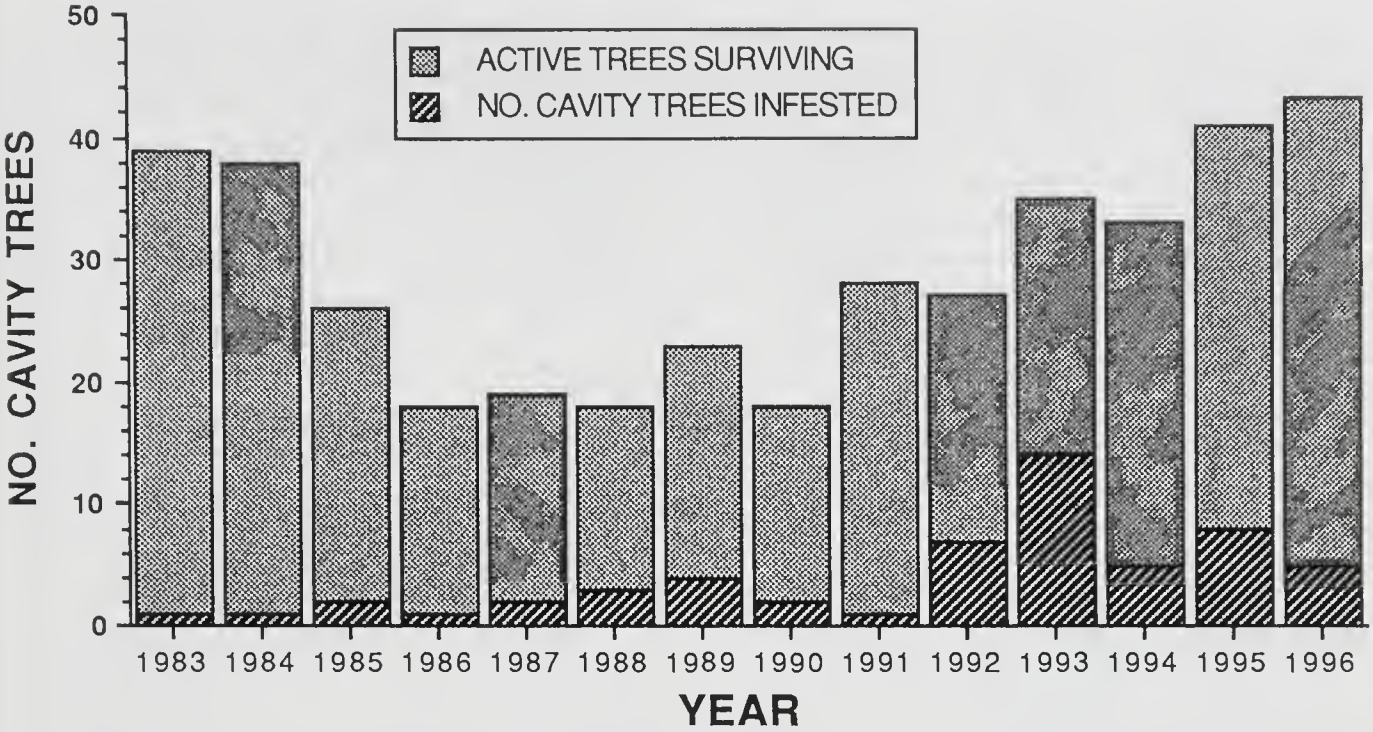

FIG. 1. Number of active Red-cockaded Woodpecker cavity trees and the number of cavity trees infested and killed by southern pine beetles on the northern portion of the Angelina National Forest from 1983 through 1996.

active cavity trees (34%) had been nest trees during the preceding breeding season, 15 (47%) had been roost trees for several years, and in 6 (19%) cavity trees, cavities had been completed just prior to infestation. Relative to their availability, nest trees on the northern portion of the Angelina National Forest were infested at a higher rate than active cavity trees used only for roosting ($\chi^2 = 4.6$, $P = 0.032$).

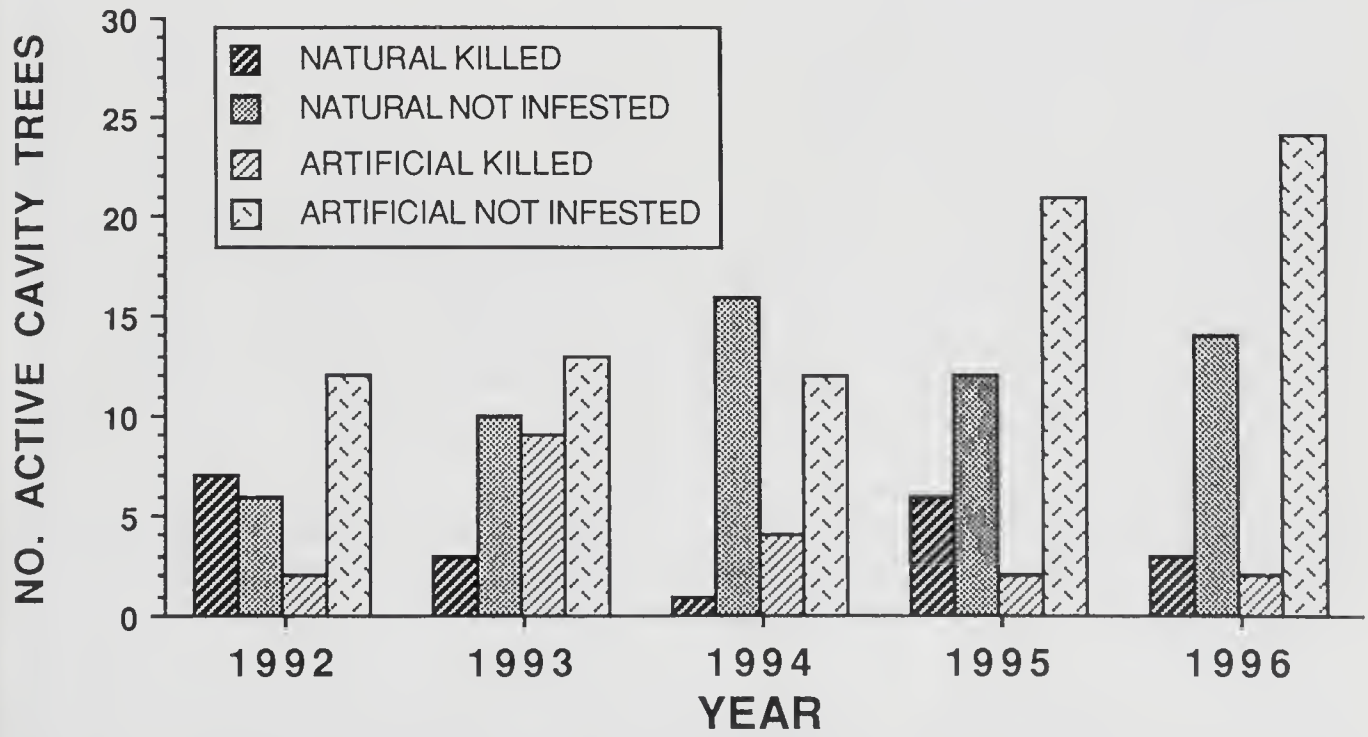

FIG. 2. The number of active Red-cockaded Woodpecker cavity trees with artificial and natural cavities in loblolly and shortleaf pines compared to the number infested and killed by southern pine beetles in eleven cavity-tree clusters on the northern portion of the Angelina National Forest between 1992 and 1996.

During the 5-year study, 20 (25.6%) natural cavity trees (78 cavity-tree years) were killed by southern pine beetles whereas 19 (18.8%) artificial cavity trees (101 cavity-tree years) were killed. Pines with natural cavities and pines with artificial cavities did not differ in the rate at which they were infested by southern pine beetles (Fig. 2; 25.6% vs 18.8%, $\chi^2 = 0.84$, adjusted for continuity, $P > 0.05$).

The recency of natural cavity completion and occupation of artificial inserts by woodpeckers, both of which included the excavation of a series of resin wells around the cavity entrances, affected the likelihood of bark beetle infestation. Over the 5-year period between 1992 and 1996, 24.5% of active cavity trees (24 of 98) were infested and killed within one year of natural cavity completion or use of cavity inserts, whereas only 7.9% of active cavity trees (13 of 164 cavity-tree years) were killed after the first year of their completion or use, respectively ($\chi^2 = 13.9$, $P = 0.001$).

Cavity-tree mortality occurring in pines with artificial cavity inserts (31.1%) during the first year of occupation was not significantly greater than mortality in newly completed natural cavity trees (18.9%; $\chi^2 = 1.97$, $P > 0.05$). However, during the four years following insert occupation or natural cavity completion, only 1.39% of the cavity trees with artificial inserts (1 of 72 cavity-tree years) were killed by bark beetles compared to 13.04% of natural cavity trees (12 of 92 cavity-tree years; $\chi^2 = 7.52$, $P = 0.006$). This suggests that active cavity trees with inserts that survive their first year have a high probability of surviving at least four more years.

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees on the northern portion of the Angelina National Forest was positively correlated with outbreaks of southern pine beetles in the surrounding forest stands (Fig. 3). Cavity tree mortality was correlated with both the number of southern pine beetle spots ($r = 0.667$, $P = 0.013$) and the number of pines infested ($r = 0.673$, $P = 0.012$) in forest stands surrounding woodpecker cluster areas.

DISCUSSION

Southern pine beetle-induced mortality of Red-cockaded Woodpecker cavity trees in loblolly and shortleaf pine habitat on the Angelina National Forest and many other forests in the South has a substantial impact on the availability of woodpecker cavity trees (Conner and Rudolph 1995, Rudolph and Conner 1995). Between 1983 and 1988 the infestation of single Red-cockaded Woodpecker cavity trees by southern pine beetles averaged about 1.7 cavity trees per year on the Angelina National Forest. Subsequent to intensification of management activities during the late 1980s to halt severe woodpecker population declines, the mean number of single cavity trees infested and killed by southern pine beetles increased significantly, more than tripling that observed previously (5.7/y; see Conner and Rudolph 1995b). As suspected by Conner and Rudolph (1995b), cavity tree infestation rates are significantly correlated with outbreaks of southern pine beetles in surrounding forest stands. However, the apparent preference of southern pine beetles for active as opposed to inactive cavity trees is still not fully understood (Conner and Rudolph 1995b, Rudolph and Conner 1995). Because of these substantial cavity-tree losses to bark beetles and the extensive use of artificial cavities by Red-cockaded Woodpeckers, most cavity trees currently used by the woodpeckers on the northern portion of the Angelina National Forest contain artificial cavities. Fortunately, Red-cockaded Woodpeckers roosted and nested readily in artificial cavities relative to natural cavities during our study and other previous studies (Copeyon 1990, Allen 1991). The importance of this management technique for Red-cockaded Woodpecker recovery in areas where bark beetles are abundant is obvious.

Our hypothesis that pines with artificial cavity inserts would be more susceptible to southern pine beetle infestation than natural cavity trees was incorrect. Artificial cavity trees were not infested and killed by southern pine beetles more or less often than natural cavity trees. This suggests that characteristics used by forest biologists on the Angelina National Forest to select pines for cavity insert installation (open boles and at least 38 cm diameter at 6 m above the ground) may not have been substantially different from those used by Red-cockaded Woodpeckers during their selection of natural cavity trees. Clearly, forest management is not creating a biological sink for Red-cockaded Woodpeckers by installing cavity inserts to re-

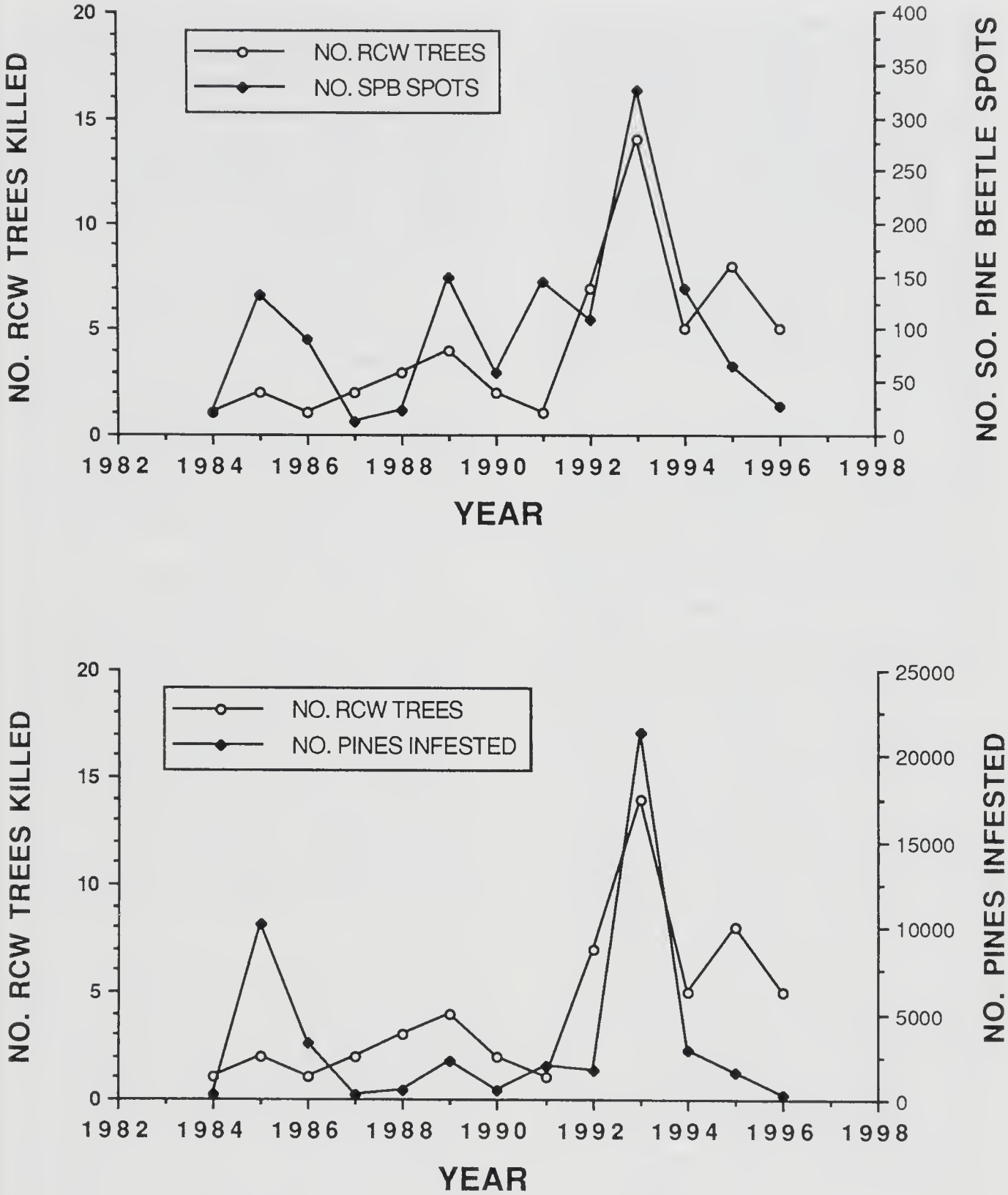

FIG. 3. The number of single Red-cockaded Woodpecker cavity trees that were infested and killed by southern pine beetles (SPB) versus the number of beetle infestations (top) and the number of pines infested by beetles (bottom) on the northern portion of the Angelina National Forest from 1983 through 1996.

place lost natural cavity trees and provide sites for woodpecker population expansion. In fact, loblolly and shortleaf pines chosen by biologists to be artificial insert trees that survived the first year of use by Red-cockaded Woodpeckers had a lower probability of being infested by bark beetles than occupied natural cavity trees. The reason for the lower infestation rate of occupied, insert cavity trees after the first year remains unknown.

Newly completed natural cavities and recently activated artificial cavities were infested at a greater frequency than cavity trees that had been active for more than one year. This was particularly true for trees with cavity inserts, suggesting that effective use of southern pine beetle repellents such as the pheromone verbenone (Payne and Billings 1989, Billings and Upton 1993) and the host tree volatile phenylpropanoid 4-allylanisole (Strom et al. 1995, Hayes et al. 1996) during the first year of insert use by Red-cockaded Woodpeckers may substantially reduce bark beetle-induced mortality to cavity trees containing artificial inserts.

There are several possible reasons why recently activated insert trees had a higher mortality rate than newly completed natural cavity trees. Excavation of natural cavities can take an extended period of time, often as much as 2 to 6 years (Conner and Rudolph 1995a). During cavity excavation and the gradual inclusion of resin wells around the cavity entrance the pine tree may have time to respond to the wounding by adding radial traumatic resin ducts and increasing resin production (Gerry 1922, Hodges et al. 1979, Nebeker et al. 1988, Ross et al. 1997). When installed cavity inserts are used by Red-cockaded Woodpeckers, the process of installation and resin well excavation often occurs in a fairly short period of time (less than a week to several months). Resin produced over a short period of time following an initial wounding is thought to be preformed resin (Nebeker et al. 1988) and not elevated production resulting from a wounding response (Gerry 1922, Harper and Wyman 1936). This sudden wounding of pines with cavity inserts followed by immediate use and resin well excavation by Red-cockaded Woodpeckers may increase their relative susceptibility to bark beetle infestation by reducing the pine's preformed resin. Excessive wounding of pines during turpentining for naval stores weakened pines and occasionally precipitated attack by bark beetles (Wyman 1932).

A significantly higher percentage of cavity trees (artificial and natural) killed by southern pine beetles had been nest trees within one year of beetle infestation. Cavity trees used for nesting are probably the most important trees for woodpecker groups and typically have numerous resin wells that produce copious amounts of fresh pine resin (R. Conner, C. Rudolph, and D. Saenz, pers. obs.). Previous research has demonstrated that active cavity trees are killed at a higher rate than inactive cavity trees (Conner and Rudolph 1995b, Rudolph and Conner 1995). The amount of resin produced by loblolly and shortleaf pines is highly variable depending in part on tree growth form, soil factors, moisture, and season of year (Schopmeyer and Larson 1955; Lorio 1986; Ross et al. 1993, 1995). The apparent attractiveness of active cavity trees with copious resin flow to southern pine beetles suggests that some component of resin volatiles, the amount of resin volatiles produced, or stress exerted on the pines by extensive resin well excavation may increase the preference/vulnerability of such cavity trees to southern pine beetle attack.

Southern pine beetles are attracted to and aggregate on pines where the resin volatile alpha-pinene (a major component of pine resin) and the beetle pheromone frontalin are present. The combination of these two chemicals serves as a strong attractant for southern pine beetles (Thatcher et al. 1980). Alpha-pinene, alone, does not appear to serve as a primary attractant to southern pine beetles (Thatcher et al. 1980, Billings 1985). Thus, it is somewhat perplexing why southern pine beetles are attracted to active loblolly and shortleaf pine cavity trees at a higher rate than to inactive cavity trees.

Site disturbance (Coulson et al. 1986, Flamm et al. 1993) and lightning strikes (Coulson et al. 1983, Lovelady et al. 1991) have been shown to be associated with the infestation of pines by southern pine beetles. Such disturbances apparently increase the attractiveness of pines for an initial attack by southern pine beetles. Woodpecker excavation of resin wells on cavity trees may sufficiently stress loblolly and shortleaf pines that they take on characteristics of pines suffering other types of stress.

The mechanism by which southern pine beetles select Red-cockaded Woodpecker cavity trees for initial attack may relate in part to the pine's production of allylanisole. This host volatile, produced by healthy pines, is known to inhibit infestation by southern pine beetles and other bark beetles (Hayes and Strom

1994, Hayes et al. 1994). Reduced levels of allylanisole have been associated with southern pine beetle attack and successful infestation of pines. Research is needed to evaluate the relative contributions of allylanisole reduction and alpha-pinene elevation resulting from Red-cockaded Woodpecker activity at resin wells toward increasing the attractiveness of pines to southern pine beetles.

ACKNOWLEDGMENTS

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HOME RANGE SIZE AND FORAGING HABITAT OF RED-COCKADED WOODPECKERS IN THE OUACHITA MOUNTAINS OF ARKANSAS

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ABSTRACT.—We obtained data for 23 habitat characteristics from plots at foraging sites of five groups of Red-cockaded Woodpeckers (*Picoides borealis*) and compared to randomly selected plots. Five groups occupied an average home range size of 24.82 ha. The birds foraged mainly in large pines having high crown volume and a long exposed bole. Foraging birds also favored stands with little understory and open spacing between foraging trees and neighboring ones. Shortleaf pine (*Pinus echinata*) was used in foraging 95% of the time over hardwoods. Woodpecker home range sizes in this shortleaf pine habitat were much smaller than in other types of forests. This may be due to the physical attributes of shortleaf pines combined with the ridged topography of the Ouachita Mountains. The vegetational requirements for foraging stressed the largest pines, open forest, and reduced hardwood understory, thus agreeing with other foraging studies of Red-cockaded Woodpeckers.
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The numerous studies of Red-cockaded Woodpeckers (*Picoides borealis*) have almost all been conducted in areas of level terrain and in forests dominated by either longleaf (*Pinus palustrus*) or loblolly pine (*Pinus taeda*), or both. Our study, conducted in the Ouachita National Forest in western Arkansas, is quite different in that the terrain was characterized by steep ridge and ravine topography and shortleaf pine (*Pinus echinata*) was the only pine. Our objective was to gain information on home range size and foraging habitat for the endangered woodpecker in this different environment.

STUDY AREA AND METHODS

Study area.—The study site was in Scott County, in the Ouachita National Forest of west-central Arkansas, a well forested area typified by shortleaf pine stands managed for timber production. It is in the Fourche Mountain subdivision of the Ouachita Mountains (Shepherd 1984) consisting of long, narrow, east-west running ridges with steep relief on sandstone and shale bedrock. Shortleaf pine dominates the forest overstory while post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*) and hickories (*Carya* spp.) comprise the understory.

This area contains the only known Red-cockaded Woodpeckers in the Ouachita Mountains of western Arkansas. Burnside (1983) found two active clusters (colonies) in the area in the late 1970s. Now about 14 active clusters containing 30–35 birds are known, some outside of Scott County.

Home range.—In February, 1990, 26 Red-cockaded Woodpeckers were captured and banded using unique combinations of both numbered aluminum U.S. Fish and Wildlife Service bands and plastic color bands. This allowed field identification of each bird. Five of these woodpecker groups (clans) were selected for study, designated groups A–E, each having a pair of adult birds at the beginning of the study.

Observations of Red-cockaded Woodpecker foraging activity and group movements were conducted on a daily basis from from 22 May 1990 through 16 August 1990 and then limited to one or two days per week from 6 October 1990 to 16 February 1991. Observations of foraging activity lasted from 2–6 h at various times during the day. Length of observations varied because of the difficulty in maintaining constant contact with individual birds, particularly in the post-breeding period when the birds were away from cluster sites much of the day and frequently obstructed from view by deciduous vegetation. Marked birds were viewed at distances varying from 5–50 m, to avoid behavior modification from the observer's presence.

Trees at the periphery of the home ranges were marked with plastic flagging and when range limits were fully characterized, these trees were accurately recorded on topographic maps. Home range sizes were determined using a computer digitizing method to measure the area included within mapped convex polygons formed by connecting adjacent boundary trees with straight lines. This is the commonly used minimum area method (Mohr 1947), useful in comparing with results of other studies, including results obtained from using Global Positioning Systems (Franzreb and Barnhill 1995). Sherrill and Case (1980) noted the terms territory and home range are used interchangeably by most authors, but suggested that territory implies a defended area traversed in daily foraging. The

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term home range will be used exclusively in the present study to indicate area used for all the woodpecker activities.

Foraging habitat.—Following the method of James et al. (1981), modified from James and Shugart (1970), vegetational characteristics were measured in circular plots centered on trees within home ranges where Red-cockaded Woodpeckers were found foraging. There were a total of 110 such foraging trees from the five woodpecker home ranges. These sites were initially located for later analysis by observing individual foraging woodpeckers and marking trees used at approximately 15 min intervals.

The habitat samples were 0.04 ha (0.1 acre) circles centered at the foraging tree in which all trees and shrubs with a diameter at breast height (DBH) greater than 7.6 cm (3 in.) were counted, trunk DBH measured, and tree identified as to hardwood or pine. Using a reach stick (James and Shugart 1970) to measure DBH, these trees and shrubs were separated into the following DBH size classes: 7.6–15.2 cm (3–6 in.), 15.2–22.9 cm (6–9 in.), 22.9–30.5 cm (9–12 in.), 30.5–38.1 cm (12–15 in.), and >38.1 cm (>15 in.). Shrub density was measured by counting woody stems less than 7.6 cm (3 in.) in diameter intercepted at waist height in two, 30.5 cm (1 ft.) wide orthogonal transects across the diameter of each plot (22.6 m or 74 ft.) oriented in cardinal compass directions. Using a clinometer, average canopy height, average understory height (shrubs and trees <7.6 cm DBH), and height of the selected foraging tree were measured in each plot.

Data obtained from the foraging tree (center tree of each plot) included type of tree (pine or hardwood), height and DBH, lower crown height, crown diameter, crown volume, number of limbs below the crown, and lowest limb height. Crown volume was calculated using a modified formula for the volume of a cylinder (James et al. 1981): $V = \frac{1}{2} \pi (D^2) \times (H_t - H_l)$, where V = crown volume, D = average crown diameter, H_t = tree height, and H_l = lower crown limit. This formula was modified to calculate a laterally distended cylinder, which more closely represents the actual shape of the crown of the trees. Distance from a foraging tree to its nearest neighbor of equal or greater DBH was noted as was distance to nearest neighbor greater than 7.6 cm DBH. This gives information on spacing of trees of the same size (or greater) as the foraging tree and also spatial distribution of all trees in the foraging area.

Foraging habitat samples were compared with an equal number (110) of random (control) samples representing available habitat in the study area. A random sample was located 100 m (328 ft.) from each foraging tree in a direction indicated by a blind twist of a compass dial. The closest tree greater than 7.6 cm DBH at that site became the center tree for a random plot, using the same methods as for foraging trees.

Data analysis.—Data obtained from vegetational samples were analyzed using Wilcoxon Matched-pairs Signed-ranks Tests to compare habitat factors selected by Red-cockaded Woodpeckers with random samples. Also, Principal Component analysis, Logistic Regression analysis, and Discriminant Function analysis were performed on the same habitat data. A variance stabilization procedure (VARSTB) was applied prior to performing Discriminant Function analyses. Tests ($\alpha = 0.05$) were performed using Statistical Analysis System (SAS Institute 1985) software.

RESULTS

Home range.—Estimates of home range size for each of the groups of Red-cockaded Woodpeckers was as follows: Group A = 19.37 ha, Group B = 42.54 ha, Group C = 17.06 ha, Group D = 24.58 ha, and Group E = 20.54 ha.

Habitat.—Analysis of the 23 vegetational characteristics (Table 1) showed that differences related mainly to the foraging tree. Characteristics that were significantly greater in Red-cockaded Woodpecker foraging plots than in control plots were: center tree height and diameter (DBH), lower crown height, crown diameter, crown volume, number of limbs below the crown, and lowest limb height. The woodpeckers commonly foraged in pines while hardwoods were significantly more common at the center of random plots (Table 1). Distance to the nearest neighbor of equal or greater DBH from the center tree and average canopy height of the surrounding forest was significantly greater in woodpecker foraging plots than in random plots. The presence at foraging sites of fewer hardwoods in 7.6–15.2 cm (3–6 in.) DBH and 15.2–22.9 cm (6–9 in.) DBH size classes was significant. These last four characteristics relate to the greater forest maturity at woodpecker foraging sites than in the random plots.

Red-cockaded Woodpeckers were almost totally restricted to shortleaf pine when foraging, selecting pines 95% of the time, hardwoods 5% of the time, whereas pines constituted 60% of the forest structure, hardwoods 40%. Only the largest pines [defined as those trees >30.5 cm DBH since few truly large shortleaf pines (>50.8 cm DBH) exist in the study area as a result of extensive regional logging in the early 1900s] of those available were heavily used by the individual woodpecker groups (Fig. 1). A comparison of the usage of five size classes of shortleaf pines by the woodpeckers and the overall availability of these pines (Fig. 2) stresses the importance of larger pines in foraging. There was nearly

TABLE 1. Analysis of 23 vegetational characteristics in the foraging habitat of Red-cockaded Woodpeckers in the Ouachita National Forest, Arkansas.[a]

Vegetational characteristics	Foraging plot mean	Random plot mean	*P*-value[b] (α = 0.05)
Center tree type[c]	0.06	0.35	0.0001
Center tree height (m)	21.78	17.63	0.0001
Center tree DBH (cm)	35.08	27.81	0.0001
Lower crown height (m)	13.02	10.06	0.0001
Crown diameter (m)	7.02	6.08	0.0029
Crown volume (m^3)	825.65	611.38	0.0054
Distance to nearest neighbor of = or > DBH (m)	6.26	5.41	0.0388
Distance to nearest neighbor >7.6 cm DBH (m)	9.82	9.92	>0.05
Number of limbs below crown	1.42	0.80	0.0013
Lowest limb height (m)	11.35	9.28	0.0001
Pines 7.6–15.2 cm DBH (No. of trees)	1.96	1.30	>0.05
Pines 15.2–22.9 cm DBH	1.80	1.55	>0.05
Pines 22.9–30.5 cm DBH	2.17	1.93	>0.05
Pines 30.5–38.1 cm DBH	2.35	1.97	>0.05
Pines >38.1 cm DBH	1.41	1.00	>0.05
Hardwoods 7.6–15.2 cm DBH (No. of trees)	4.85	5.99	0.0279
Hardwoods 15.2–22.9 cm DBH	1.67	2.28	0.0309
Hardwoods 22.9–30.5 cm DBH	0.73	0.80	>0.05
Hardwoods 30.5–38.1 cm DBH	0.36	0.52	>0.05
Hardwoods >38.1 cm DBH	0.25	0.32	>0.05
Shrub density measure (No. of stems)	4.91	5.00	>0.05
Average canopy height (m)	19.42	18.63	0.0301
Average understory height (m)	2.19	2.45	>0.05

[a] First 10 characteristics pertain to the center tree.
[b] Wilcoxon Matched-pairs Signed-ranks Test.
[c] Value based on assigned values of pine = 0 and hardwood = 1.

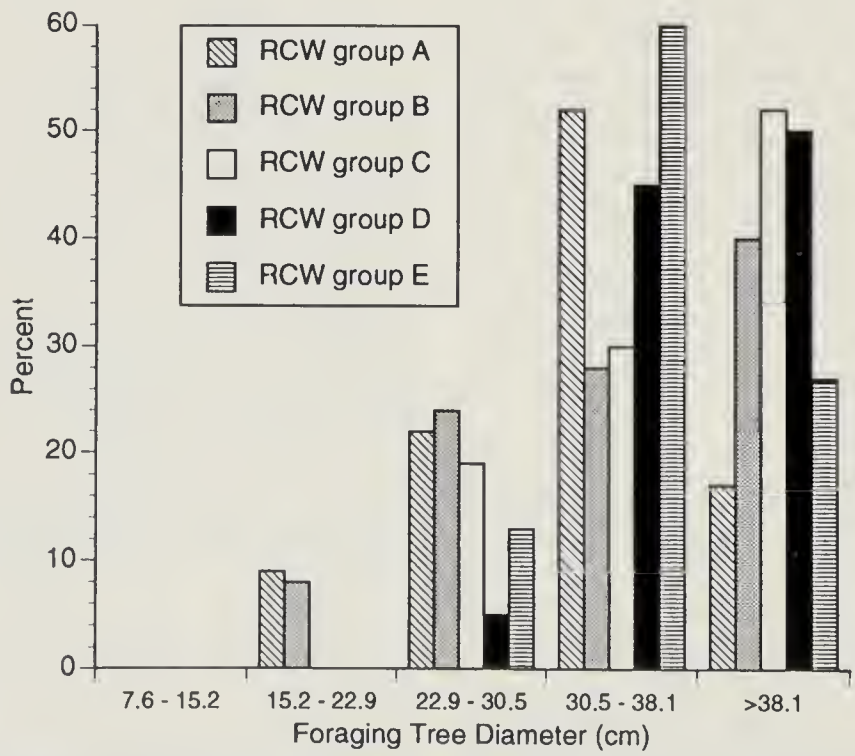

FIG. 1. Percent foraging use of five size classes of shortleaf pines by five groups of Red-cockaded Woodpeckers (RCW) in the Ouachita National Forest, Arkansas (110 samples).

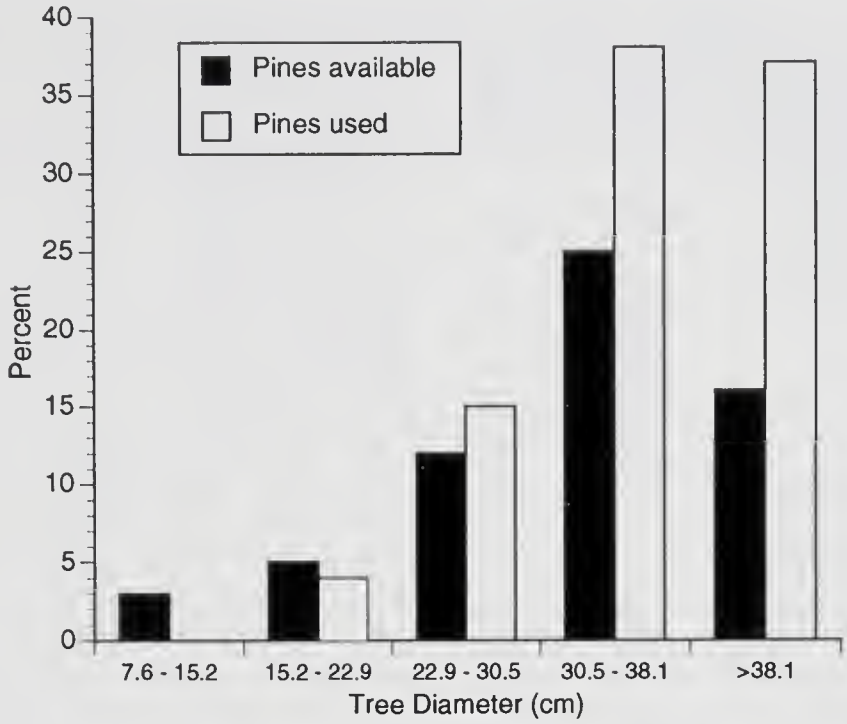

FIG. 2. Percent shortleaf pine usage (110 foraging trees) in five size classes selected by five groups of Red-cockaded Woodpeckers compared to percentage of overall shortleaf pine availability (110 random trees).

equal use of both the two largest sizes of pines (n = 104 combined) even though the larger of the two categories contained relatively the smallest number of pines (n = 38). Although hardwoods (n = 14) were much less common than pines and were mostly in the smallest size class, the few used in foraging were larger trees.

Densities of shortleaf pines more than 30.5 cm DBH/ha were determined for each home range along with the total number of stems greater than 30.5 cm DBH/home range (noted in parentheses) as follows: Group A = 67.0 (1297.8), Group B = 64.0 (2722.6), Group C = 97.25 (1659.1), Group D = 139.5 (3428.9), and Group E = 73.5 (1509.7). Mean number of stems greater than 30.5 cm DBH/ha for all groups = 88.25 and mean number of stems greater than 30.5 cm DBH/home range for all groups = 2123.6.

Principal Component analysis combining foraging and random habitat samples of all five groups of Red-cockaded Woodpeckers (Table 2) showed that six of the same important tree size characteristics that were statistically significant in Table 1 were highly correlated with the first Principal Component (PC-I). Because PC-I always represents the greatest variance in a system analyzed, this means that tree size attributes of the center trees in sample plots were the most variable components in the habitat of the study area. Because a zero (0) was assigned if the center tree was a pine, and a one (1) assigned to hardwood center trees, the high negative correlation with PC-I for center tree type (Table 2) indicates a preference for pines in foraging. The scatter of individual plots along this axis showed that the random plots were distributed along the whole axis from small to large sized center trees, the center trees being either hardwood or pine. However, the woodpecker foraging plots were highly concentrated at the end characterized by big pine trees. Therefore, PC-I (Table 2) supports the findings obtained from paired comparisons of vegetational characteristics (Table 1). PC-II emphasizes crown size, average canopy height, and distance between trees (Table 2), which pertains to degree of forest openness. This axis did not separate the foraging and random plots. Logistic Regression analysis also confirmed through a stepwise elimination procedure that center tree size, in this case tree height, was the statistically significant factor separating woodpecker foraging from non-foraging sites.

The situation shown by Principal Components was tested using stepwise Discriminant Function analysis, which showed center tree DBH and height as well as tree type and num-

TABLE 2. Results of Principal Component analysis of 23 vegetational characteristics, comparing foraging sites with random samples, for five combined groups of Red-cockaded Woodpeckers in the Ouachita National Forest, Arkansas.[a]

Vegetational characteristics	PC-I	PC-II
Center tree type (pine or hardwood)	−0.65[b]	0.34
Center tree height	0.92	−0.14
Center tree DBH	0.86	0.25
Lower crown height	0.83	−0.33
Crown diameter	0.58	0.53
Crown volume	0.53	0.59
Distance to nearest neighbor of = or > DBH	0.47	0.60
Distance to nearest neighbor >7.6 cm DBH	0.29	0.44
Number of limbs below crown	0.09	0.02
Lowest limb height	0.76	−0.32
Pines 7.6–15.2 cm DBH	−0.18	−0.09
Pines 15.2–22.9 cm DBH	−0.07	−0.22
Pines 22.9–30.5 cm DBH	0.17	−0.48
Pines 30.5–38.1 cm DBH	0.32	−0.47
Pines >38.1 cm DBH	0.03	−0.07
Hardwoods 7.6–5.2 cm DBH	−0.36	0.02
Hardwoods 15.2–22.9 cm DBH	−0.42	0.08
Hardwoods 22.9–30.5 cm DBH	−0.23	0.02
Hardwoods 30.5–38.1 cm DBH	−0.16	−0.04
Hardwoods >38.1 cm DBH	−0.17	−0.02
Shrub density measure	0.12	0.38
Average canopy height	0.23	−0.69
Average understory height	−0.32	0.07

[a] First 10 characteristics listed pertain to sample plot center tree.
[b] Underlined values indicate high correlation ($P < 0.05$) with the respective factors.

ber of limbs below the crown were significant in separating woodpecker usage and control sites, again confirming a dependance on tall, large diameter pines by Red-cockaded Woodpeckers for foraging. The discrimination was noteworthy in that the analysis correctly classified 82% of the foraging plots and 87% of the random plots out of the 110 samples of each type.

DISCUSSION

Home range.—The average home range size of 24.82 ha found in this study was much smaller than the overall mean size of 76.13 ha calculated from this plus 14 previous studies on Red-cockaded Woodpeckers (Table 3). The two prior findings that were closest to our results were 17.2 and 32.1 ha reported by Crosby (1971) and Sherrill and Case (1980), respectively.

In evaluating this large difference in home range size, the number of birds in each group studied must be considered because an increase in group size could cause an increase in home range size. However, Nesbit et al. (1978) found that a small group does not necessarily inhabit a small home range. In that case three groups containing two to four birds occupied an average home range size of 69.8 ha. This suggests that other factors affect home range size, such as habitat quality and forest type (e.g., dominant pine species).

Previous studies were conducted in forests of pine other than shortleaf, except for Wood (1983). Most show rather large home range sizes (Table 3) compared to our study. Perhaps the structural and growth characteristics of shortleaf pine make it possible for home ranges to be smaller than in longleaf or loblolly pine forests. According to Mattoon (1915), shortleaf pines typically have crowns composed of numerous small branches forming a narrow pyramidal shape permitting the high density of trees characterizing shortleaf pine forests. The crown of longleaf pine is similar to that of shortleaf at first but in mature trees the crowns broaden, lowering tree density in longleaf stands compared to shortleaf stands. Loblolly pine maintains a dispersed, large branched crown throughout its life resulting in less tree density than shortleaf pine.

The above suggests shortleaf pines may have more branch surface area in the crown than other pines, providing relatively greater area for woodpecker foraging, possibly reducing the number of trees needed in the home range. Add to this the observation that shortleaf pines grow more densely than other pines. This combination of increased foraging area and tree density in shortleaf stands could provide needed resources in smaller areas of shortleaf pine than in loblolly and longleaf stands.

Another reason for smaller home ranges in this study may be the topography of the Ouachita Mountains. When the home ranges were positioned on a topographic map, each home range nearly fit in ravines between ridge lines, rarely crossing over to the opposite side of a ridge. A possible reason for this home range configuration is that Red-cockaded Woodpecker groups are quite social and vocal when foraging (Ligon 1970). Foraging on op-

TABLE 3. Comparison of Red-cockaded Woodpecker home range sizes from 15 studies.

Study and location	Season[a]	No. groups	Birds per group	Ave. home range size (ha)	Range in size (ha)	Forest type[b]
Baker (1971)						
Florida	S	1	8	65.6	—	MX
Crosby (1971)						
Florida	S	2	2	17.2	14.4–20.0	LO
DeLotelle et al. (1987)						
Florida	Y	6	2–8	150.0	116.2–198.8	LO
DeLotelle et al. (1995)						
Florida	Y	13	1–3	129.0	86.0–161.0[c]	LO
Epting et al. (1995)						
Florida & Georgia	Y	18	?	79.8	21.0–107.0	MX
Franzreb & Barnhill (1995)						
South Carolina	S, W	7	?	49.7	14.5–93.6	MX
Hooper et al. (1982)						
South Carolina	Y	24	2–6	86.9	34.0–225.0	MX
Jackson & Parris (1995)						
Louisiana	Y	8	1–5	135.0	109.0–170.0[d]	MX
James et al. (1981)						
Arkansas	S	2	3–5	56.7	35.7–86.6	LB
Nesbit et al. (1978)						
Florida	W	3	2–4	69.8	58.4–91.4	MX
Repasky & Doerr (1991)						
North Carolina	Y	2	?	159.5	139.0–180.0	LO
Sherrill & Case (1980)						
South Carolina	W	4	2–8	32.1	20.6–43.7	LO
Skorupa & McFarlane (1976)						
South Carolina	S, W	2	2–4	41.9	17.6–65.8	MX
Wood (1983)						
Oklahoma	S	1	4	44.1	—	SL
Present study						
Arkansas	Y	5	2–3	24.8	17.1–42.5	SL
	Overall average size			76.1 ha		

[a] Seasons: S = summer, W = winter, Y = year-round.
[b] Forest types: LO = longleaf pine, LB = loblolly pine, SL = shortleaf pine, MX = mixed pine species.
[c] Territory sizes only.
[d] Pre-disturbance home range sizes.

posite sides of ridges may prevent communications between group members thus confining home ranges to individual ravine watersheds.

Habitat quality may affect the home range size in that small home ranges could occur in better habitat. DeLotelle et al. (1987) indicated average home range sizes in central Florida were larger than in South Carolina where habitat was considered better. Population densities of Red-cockaded Woodpeckers are low in the Ouachita Mountains so there would be low competition for optimal habitat. Thus, it is expected that these birds would occupy the best available microhabitats, which often happens in other avian species (Wiens 1973). Having optimum habitat available these Red-cockaded Woodpeckers may be showing an inverse relationship between quality of habitat and size of home range (i.e., the better the habitat the smaller the home range). Davis (1982) found this relationship existed between habitat quality and the breeding and nonbreeding territory size in Belted Kingfishers (*Megaceryle alcyon*).

Annual duration of home range observations can affect the outcome of range delineations. Year-round observations often result in a more accurate outline of the total home range occupied by Red-cockaded Woodpecker groups (Hooper et al. 1982) while studies that use partial year data may not provide as precise a depiction of the bird's home range. Our study, though not continuous year-round, does

combine data from spring and summer when home ranges tend to be smaller with data from fall and winter when home ranges are larger.

Habitat.—Foraging habitat data collected for the five groups of Red-cockaded Woodpeckers indicate a overwhelming preference for large (mean height = 21.78 m, mean DBH = 35.08 cm) shortleaf pines as a foraging substrate (Tables 1 and 2; Figs. 1 and 2). This supports previous findings showing a preference for large pine trees in foraging (Skorupa and McFarlane 1976, Hooper and Lennartz 1981, Epting et al. 1995). Other vegetational characteristics were preferentially selected too by Red-cockaded Woodpeckers (Table 1) including trees with a high exposed bole (mean height of lowest limb = 11.35 m), wide crown diameter (mean crown diameter = 7.02 m) and high crown volume (mean crown volume = 825.65 m^3). In total, all these characteristics emphasize the use of large pine trees by foraging Red-cockaded Woodpeckers.

Space between trees with a diameter equal to or greater than that of foraging trees also proved significant (Table 1), with a mean distance between trees of 6.26 m, indicating a greater "openness" between trees than what was found in the control samples (mean distance between trees in control = 5.41 m). Also, the paucity of small hardwoods (particularly in the range of 7.6–22.9 cm DBH) in foraging samples (Table 1) indicated that, as in other types of pine forests, Red-cockaded Woodpeckers prefer foraging areas that are open without small or midsized hardwood understory (Ligon 1970, Hooper et al. 1980, Hovis and Labisky 1985). The vegetational cline on PC-II also stressed this "openness" (Table 2) but actually foraging and random trees were not separated on this axis. Therefore, forest openness may not be as important as having large pine trees for foraging Red-cockaded Woodpeckers.

In nearby McCurtain County in southeast Oklahoma, Wood (1983) showed a significantly lower midstory vegetation height in the "use" (used for woodpecker foraging) compared to "non-use" areas or less intensively used areas. The present study supports Wood's data in midstory height (Table 1). However, Wood found Red-cockaded Woodpeckers foraged in dense overstory while our results show utilization of less dense overstory shown by the greater distance between large trees, higher lowest limb, and taller canopy height for foraging than random trees (Table 1). A probable cause for this difference is that the Wilderness Area in Wood's study is a virgin forest with a restrictive policy against fire and vegetational controls such as mechanical midstory removal and stand thinning, while the Ouachita National Forest is a managed forest that experiences vegetational control, both by fire and mechanical means. This thinning by the Forest Service, in effect, optimizes foraging habitat for the woodpeckers, allowing for selection of habitat preferences while the unmanaged Wilderness Area forces the birds to use dense pine stands with heavy mid and understory vegetation.

Red-cockaded Woodpeckers have small home ranges and rather specific foraging requirements in shortleaf pine forests. The small home range sizes shown here could be related to a combination of high habitat quality and the presence of close topographic boundaries. The foraging specificity shown by Red-cockaded Woodpeckers is a requirement of large pine trees with an open spatial arrangement between trees and small amounts of associated mid and understory vegetation. Such conditions are known to be critical for Red-cockaded Woodpecker populations in other forest types, but this is the first confirmation of its importance in a shortleaf pine forest. The almost exclusive use of pines for foraging is also supported by other studies.

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Confirmation of Nesting in Mexico for Four Bird Species from the Sierra San Pedro Mártir, Baja California

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ABSTRACT.—We document nesting of Dusky Flycatcher (*Empidonax oberholseri*), Hermit Thrush (*Catharus guttatus*), Green-tailed Towhee (*Pipilo chlorurus*), and Fox Sparrow (*Passerella iliaca*) in the Sierra San Pedro Mártir of northern Baja California. These species are relatively widespread in the mountains of southern California. Additional species recently observed in the Sierra San Pedro Mártir in summer remain as unconfirmed breeders in Baja California [Northern Saw-whet Owl (*Aegolius acadicus*) and Townsend's Solitaire (*Myadestes townsendi*)] or all of Mexico [Hermit Warbler (*Dendroica occidentalis*)].
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The highlands of the Sierra San Pedro Mártir in northern Baja California received scant ornithological coverage prior to completion of the road to the National Observatory in the 1970s. The observatory is at the summit of the eastern escarpment, at an elevation of approximately 2800 m. Richard E. Webster, Wurster, and others have made at least seven spring and summer visits to these remote mountains since 1984. Among the many significant observations accumulated in this interval are records of seven species previously unknown from Baja California in summer: Northern Saw-whet Owl (*Aegolius acadicus*), Dusky Flycatcher (*Empidonax oberholseri*), Townsend's Solitaire (*Myadestes townsendi*), Hermit Thrush (*Catharus guttatus*), Hermit Warbler (*Dendroica occidentalis*), Green-tailed Towhee (*Pipilo chlorurus*), and Fox Sparrow (*Passerella iliaca*). Excepting the owl and solitaire, which are resident in mainland Mexico, none of these species was known to nest anywhere in Mexico prior to these observations (AOU 1983, Wilbur 1987, Phillips 1991, Kratter 1992); all are known to winter in Mexico. Howell and Webb (1992, 1995) suggested that the flycatcher, thrush, and towhee probably breed in the Sierra San Pedro Mártir, but were unable to confirm nesting. We provide documentation of nesting for these three species and Fox Sparrow.

Of the other species, Erickson et al. (1994) discussed the initial saw-whet owl record (subsequently, up to three were heard along the La Tasajera road in the Sierra San Pedro Mártir 28–29 May 1994; Wurster, Kurt and Cindy Radamaker, pers. obs.); Webster and Wurster observed a Townsend's Solitaire near the National Observatory on 3 July 1987; and we observed a single male Hermit Warbler on 5 July 1993 in white fir (*Abies concolor*) forest near the National Observatory, but it did not appear to be mated.

Plant taxonomy follows Wiggins (1980).

SPECIES ACCOUNTS

*Dusky Flycatcher (*Empidonax oberholseri*).*—This species breeds in the mountains of southern California as far south as the Laguna Mountains of San Diego County, at least sporadically (Garrett and Dunn 1981, Unitt 1984, Kratter 1992). Webster (pers. comm.) first found two pairs in the Sierra San Pedro Mártir in an aspen (*Populus tremuloides*) grove about 2 km southeast of the National Observatory at 2700 m on 30 June 1984 and 1–2 singing birds were found there and at other aspen groves nearby in 1987 and 1991 (Howell and Webb 1992). Webster (pers. comm.) first confirmed nesting on 5 July 1992, when four birds he saw included one carrying food.

On 5 July 1993, we found three Dusky Flycatchers (one singing) at the above mentioned aspen grove, and four on the La Tasajera road nearby. Among the latter birds were two adults feeding young in a nest about 5–6 m

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up in a lodgepole pine (*Pinus contorta*) approximately 2 km south of the main park road at an elevation of about 2600 m. The nest sat atop a horizontal branch about 2 m out from the trunk, and considerable aspen material appeared to have been used in its construction. We observed the adults bringing food to the nest several times, but were unable to see the number or condition of young. The nest tree was part of a mixed coniferous forest of lodgepole pine, white fir, and Jeffrey pine (*Pinus jeffreyi*) in the vicinity of a meadow system and an aspen grove.

More than 20 singing, and apparently territorial, Dusky Flycatchers were observed by Wurster and K. and C. Radamaker on 29 May 1994. They were present in virtually every grove of aspen, pine, and fir lining the La Tasajera road, which meanders across the meadows of the main plateau from the observatory road south toward the La Tasajera divide.

*Hermit Thrush (*Catharus guttatus*).*—In southern California, this species breeds south to the San Bernardino and San Gabriel mountains, with occasional summer records south to the mountains of San Diego County (Garrett and Dunn 1981, Unitt 1984, Kratter 1992). In the Sierra San Pedro Mártir, up to five singing Hermit Thrushes were observed in June or July of 1984, 1986, 1987, 1991, and 1993 (Howell and Webb 1992, pers. obs.). They were near the National Observatory, primarily on north-facing slopes dominated by white fir and bordering the aspen grove at 2700 m. Nesting was confirmed on 5 July 1992 when Webster (pers. comm.) observed four birds in the same area, including one adult carrying food and one recently fledged young. Field notes by Webster and Wurster describe these birds as relatively large and pale for the species, characteristics of the mountain group of subspecies including *C. g. sequoiensis* of the Sierra Nevada and southern California.

*Green-tailed Towhee (*Pipilo chlorurus*).*—This species is a rather wide spread breeder in montane southern California, including San Diego County (Garrett and Dunn 1981, Unitt 1984, Kratter 1992). Wurster first observed a singing male at La Corona de Arriba (km 84 on the main park road, elevation 2600 m) on 4 July 1987. Howell and Webb (1992) observed four towhees (two singing birds and another pair acting agitated, as if near a nest) at 2700 m in the Sierra San Pedro Mártir on 16 June 1991.

Wurster observed a single Green-tailed Towhee at the aspen grove near the National Observatory on 5 July 1993 and we found at least two birds at La Corona de Arriba. A singing bird on 4 July 1993 was followed by two birds on 6 July, one of which was an obvious locally reared juvenile (still in streaked plumage) well seen by Alan D. Barron. The habitat where these birds were seen consisted of small meadow openings among mixed coniferous forest dominated by white fir, Jeffrey pine, lodgepole pine, and sugar pine (*Pinus lambertiana*). Meadow vegetation included lupine (*Lupinus* sp.), bracken (*Pteridium aquilinum*), and snow berry (*Symphoricarpos oreophilus*). Bracken is an important component of the nesting habitat at Cuyamaca Peak in San Diego County (P. Unitt, pers. comm.).

*Fox Sparrow (*Passerella iliaca*).*—This is a widespread breeder in montane southern California, including San Diego County (Garrett and Dunn 1981, Unitt 1984, Kratter 1992). Webster (pers. comm.) first found this species in the vicinity of La Corona de Arriba on 3 July 1992 (one *P. i. stephensi*-like individual; no evidence of breeding).

We observed six Fox Sparrows (three singing males) in the same area on 5–6 July 1993 and obtained evidence of nesting for two pairs on 6 July. The plumage and structure of all birds appeared to match *P. i. stephensi,* the breeding subspecies throughout southern California. One obvious juvenile followed an adult male and foraged on the ground between scattered brush. Another pair, over 1 km away, included a female carrying food, scolding, and driving a dusky chipmunk (*Eutamias obscurus*) from the area. We searched in vain for the nest or young of this pair. The forest habitat in these areas was similar to that described for the towhees above, but was drier and considerably more open, with only scattered trees. More significant was the different shrub layer. Fox Sparrow habitat was dominated by manzanita (*Arctostaphylos* sp.) and snow bush (*Ceanothus cordulatus*) up to 2 m high with open ground in between.

These Fox Sparrows were accomplished vocal mimics. One male routinely incorporated Olive-sided Flycatcher (*Contopus cooperi*) song phrases into the opening of its song,

while the song most often given by another was essentially a copy of the song of Black-chinned Sparrow (*Spizella atrogularis*). This imitation was close enough to our ears that we originally misidentified the song to species.

DISCUSSION

All of these nesting species were found in habitat with vegetation structure similar to that found in their typical breeding habitat in the mountains of southern California. Suitable habitat may occur in very limited patches in the Sierra San Pedro Mártir. For example, all of our observations of summer Hermit Thrushes come from a single small stand of mature white fir on a steep north-facing slope along the high eastern escarpment. There is an abundance of downed timber and scattered shrubs in the ground layer. The ground layer in other fir dominated areas is much more open. Suitable habitat for Green-tailed Towhees and Fox Sparrows is also limited. Open forest with sufficient brushy understory is apparently restricted to a narrow band paralleling, and immediately east of, the range's lower western escarpment. In contrast, Dusky Flycatcher habitat is extensive and includes all the aspen groves and numerous islands of mixed aspen, lodgepole pine, and fir lining the edges of the extensive central plateau meadow system.

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Richard E. Webster kindly shared his field notes, answered inquiries, and commented on an early draft of the manuscript. Alan D. Barron traveled to the Sierra San Pedro Mártir with us in July 1993 and was an important participant in all observations at that time. Philip Unitt provided an update on the summer status of these species in San Diego County. Steve N. G. Howell and an anonymous reviewer made useful comments on the manuscript.

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Greater Prairie-Chickens Displaying in Tree on Lek

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ABSTRACT.—I describe 23 observations of 4 Greater Prairie-chicken males displaying from a tree in eastern Kansas. This was observed on a lek located in predominantly native tallgrass prairie containing a few scattered trees. *Received 24 May 1997, accepted 5 Aug. 1997.*

Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) leks are generally on high prairie with grass cover that is relatively short compared with surrounding vegetation (Yeatter 1943; Schwartz 1944, 1945; Schroeder and Braun 1992). Leks are in open country with wide vistas (Hamerstrom et al. 1957). Displays are typically performed on the ground but have been performed on blinds and other raised positions (Schwartz 1945, Hamerstrom and Hamerstrom 1973). This note describes prairie chickens displaying in a tree.

The observed lek was in native tallgrass

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prairie in Lyon County, Kansas (96° 08′ 00″ W, 38° 32′ 02″ N). The grassland area including the lek was moderately grazed, annually burned, and interspersed with ~20% woody cover and ~10% cropland. Woody vegetation in the area was scattered eastern cottonwood (*Populus deltoides*), elm (*Ulmus* sp.), hackberry (*Celtis occidentalis*), and osage orange (*Maclura pomifera*), with eastern red cedar (*Juniperus virginiana*) invading prairie pastures or abandoned cultivated fields. Density of prairie-chicken leks in this area was ~0.12 leks/km^2.

Four prairie-chickens were observed in a 6 m high cottonwood tree when the lek was first observed on 26 March 1997. All 4 birds were "booming." On closer observation, it was found that the lek consisted of 16 males displaying on the ground beneath and north of the tree. Another 3 m high cottonwood was present 5 m from the tree being used by the prairie-chickens.

The four males in the tree were performing in part the "variant" boom as described by Grange (1948:177). This display consisted of erection of pinnae, inflation of air sacs, and snapping of the tail. The accompanying vocalizations included the staccato cackle, booming, and the whoop call (Hjorth 1970). Males on the ground performed the complete display including dancing and turning in circles.

The 4 males in the tree periodically flew to the ground to interact with the 16 males there. Each time a male flew from the tree to the ground, a male flew to the tree within a few seconds. These may have been the same or different males. The above observations were noted on 23 different mornings during peak display (~20 Mar–20 Apr). There were 4 males using the tree on all observation days. The number of males on the ground beneath the tree ranged from 16–21. A minimum of 7–10 females were observed on the ground on or near the lek. One female perched in a cottonwood tree 500 m from the lek on 2 days of observation.

This lek has been under observation for most display seasons since 1964. During that period, the lek has moved 0.8 km south of its first location. The last movement of this lek was 0.24 km southeast of its previous booming season location. Most (~80%) of the area within a 1.6 km radius of this lek is native prairie pasture.

Since all repeat observations of this booming ground were similar, it is assumed the observer did not influence use of the tree. Grange (1948) noted the "variant" boom occurring in trees "rarely" when birds were disturbed. It was, in fact, the observation of prairie-chickens in a tree from 0.8 km distance that drew the observer's attention to the whereabouts of the lek.

Use of trees by female prairie-chickens has been observed in response to intrusion and for winter budding (Schmidt 1936). Use of trees for display, to my knowledge, has only been mentioned by Grange (1948).

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Interspecific Competition Between Vultures for Preferred Roost Positions

Neil J. Buckley[1]

ABSTRACT.—I recorded the spatial distribution of Black Vultures (*Corogyps atratus*) and Turkey Vultures (*Cathartes aura*) roosting on electricity pylons in south Texas on 14 evenings. Both species clearly preferred to roost on the upper level of the pylons, and when there was little competition for space most vultures used the upper middle section. However, as densities of vultures increased, Black Vultures monopolized the upper level and Turkey Vultures became increasingly concentrated on the lower level. Although there were many potential roosting sites available on other pylons, Turkey Vultures chose to roost on the lower level of occupied pylons rather than move. Their decision to stay suggests that there is a potential cost to moving, perhaps an increased risk of predation. *Received 30 June 1997, accepted 29 Oct. 1997.*

Many birds roost communally, a behavior for which three major selective advantages have been proposed. These are: energy savings through improved thermoregulation (Brenner 1965, Chaplin 1982, Williams et al. 1991); reduced risk of predation (Lack 1968, Gadgil 1972); and enhanced foraging success, either because roosts function as information centers (Ward and Zahavi 1973; Rabenold 1983, 1987; Marzluff et al. 1996; Buckley, 1997) or they serve as assembly points for groups of foraging birds (Evans 1982, Buckley 1996). These potential benefits of communal roosting are balanced by a number of likely costs. Costs include increased exposure to parasites and diseases (Lack 1968), plumage damage caused by the droppings of birds roosting above (Yom-Tov et al. 1979), and the energetic costs of commuting between feeding sites and communal roosts.

Positions within a roost vary in quality because sites differ in their degree of exposure to the elements and in the level of protection they offer against predators. Intraspecific competition for positions within roosts has been described for a wide variety of species. Evidence that lower status birds are forced to occupy inferior positions within communal roosts has been presented for, among others, Red-winged Blackbirds (*Agelaius phoeniceus*; Weatherhead and Hoysak 1984), Rooks (*Corvus frugilegus*; Swingland 1977), and Bramblings (*Fringilla montifringilla*; Jenni 1993). This paper describes apparent interspecific competition between Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) for preferred roosting positions on electricity pylons.

METHODS

Observations were made on the 3157-ha Rob and Bessie Welder Wildlife Refuge, Sinton, Texas (28° 06′ N, 97° 22′ W). Black Vultures and Turkey Vultures are common in the area, and at night form communal roosts in trees along the Aransas River and on electricity pylons. The pylons used for roosting (Fig. 1) are about 25 m high and consist of two vertical supports topped by a superstructure. The lower level of the superstructure consists of two approximately 19 m long horizontal beams joined together by cross pieces. Above these beams, supported by a framework of girders, is a slightly more complex upper level. This is made up of three sections: an approximately 10 m long horizontal central section, two 2 m high struts, and two approximately 3.5 m long sloping sections of girder that join the upper and lower levels. Vultures roosted on the horizontal beams, the struts, and the sloping sections of the upper beam. Vultures occasionally perched on the electricity lines suspended from the

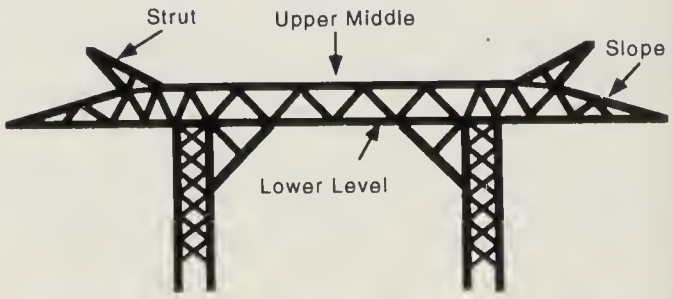

FIG. 1. Electricity pylon showing regions referred to in the text.

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TABLE 1. Spatial distribution of vultures perched on electricity pylons from October to December 1991 (winter) and in March and April 1992 (spring) on the Welder Wildlife Refuge, Sinton, Texas.

Species	Season	Site				Total
		Struts	Upper middle	Slopes	Lower level	
Turkey Vulture	Winter	8 (6.6%)	20 (16.5%)	8 (6.6%)	85 (70.2%)	121
	Spring	9 (9.9%)	54 (59.3%)	23 (25.3%)	5 (5.5%)	91
Black Vulture	Winter	57 (11.5%)	318 (64.1%)	84 (16.9%)	37 (7.5%)	496
	Spring	9 (5.7%)	135 (86%)	13 (8.3%)	0	157

struts, but rarely remained there for more than a few minutes before moving to the main structure.

In October 1991, while counting vultures roosting on the pylons, I noticed that more Turkey Vultures than Black Vultures appeared to roost on the lower level. To assess whether this was normal, I counted and plotted the positions of vultures roosting on the pylons on seven evenings between October and December 1991 ("winter"), and on seven evenings in March and April 1992 ("spring"). I used a 15–60 × 60 telescope to observe roosting birds from distances of between 200 m and 400 m, beginning counts up to 45 min before dark and repeating them every 5 min until it was too dark to identify individuals to species. Vultures were assigned to one of four locations on the pylon (Fig. 1): middle section of the upper beams (upper middle), sloping sections of the upper beams (slopes), lower beams, or struts. Because the nightly total of vultures roosting on a single pylon ranged from 4 to 136, I was able to determine the roost positions individuals occupied under a wide range of vulture densities.

RESULTS

On the 14 evenings that I observed vultures roosting on the pylons, the same pylon was occupied by birds on 11 occasions, and that pylon and the adjacent one were occupied on three evenings. Overall, 75.5% of vultures recorded (653 of 865) were Black Vultures. Significantly more vultures (both species combined) used the pylons for roosting in winter ($\bar{x}$ = 88.1, SE = 10.0) than in spring ($\bar{x}$ = 35.4, SE = 7.5; t = 4.21, df = 12, $P < 0.01$). Some vultures were present in the roost several hours before dark, but most arrivals occurred in the last hour of daylight, with more than 50% of individuals of both species entering the roost in the last 30 min before nightfall.

Vultures strongly preferred the upper level of pylons over the lower level (Table 1). In spring, when few vultures used pylons for roosting, all Black Vultures perched on the upper level, as did most Turkey Vultures (94.5%). In winter, when the pylons were crowded, most Black Vultures (92.5%) still roosted on the upper level, but a significantly lower proportion of Turkey Vultures (29.8%) did so than in spring [χ^2 (with Yates' correction) = 86.5, df = 1, $P < 0.001$].

Most vultures perched on the upper middle section of the pylons, especially when densities of roosting birds were low. In spring, 86% of Black Vultures and 62.8% of Turkey Vultures roosting on the upper level used the middle section. Similarly, 69.3% of Black Vultures and 55.6% of Turkey Vultures roosted on the upper middle section in winter. In contrast, the struts and slopes were used by fewer vultures. In winter, 28.4% of Black Vultures roosted in these areas, but in spring, when fewer birds were present, only 14% of Black Vultures roosted there (χ^2 = 16.78, df =1, $P < 0.001$). There was no significant difference between winter and spring in the proportion of Turkey Vultures that roosted on the struts (χ^2 = 0.76, P = 0.384; Table 1). However, a significantly greater percentage of Turkey Vultures roosted on the slopes in spring (25.3%) than in winter (6.6%), part of the much greater numbers then roosting on the upper level (χ^2 = 14.49, df = 1, $P < 0.001$).

The more vultures that roosted on the pylons, the greater the proportion (arcsine-transformed) of Turkey Vultures that perched on the lower level (Pearson's r = 0.9464, $P <$ 0.01, Fig. 2). When fewer than 50 vultures were present, 86 of 91 Turkey Vultures (94.5%) roosted on the upper level, but when more than 50 vultures were present only 36 of 121 (29.7%) roosted there (χ^2 = 89.2, df = 1, $P < 0.001$). This pattern does not result from Turkey Vultures being the last to arrive at the roost and so having to occupy whatever places remain. Although similar numbers of sites were available to them, Turkey Vultures and Black Vultures arriving just before dark

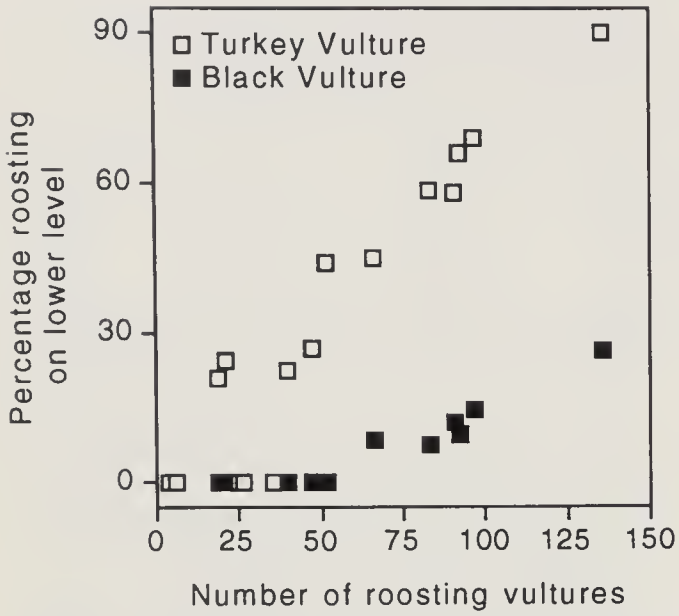

FIG. 2. Relationship between overall number of vultures (of both species) present on a pylon and arcsine transformed proportion of Black and Turkey vultures roosting on the lower level.

differed in their landing sites. In the last 15 min before dark (on six days in winter when from 66 to 136 vultures roosted on the pylons), 91 of 108 Black Vultures (84.2%), landed on the upper level compared to only 5 of 47 Turkey Vultures (10.6%; $\chi^2 = 75.3$, df = 1, $P < 0.001$).

On three nights the birds occupied two adjacent pylons. In one instance, the birds initially settled on a single pylon, but following a disturbance (cause unknown) redistributed themselves between two pylons. In the other two cases, the birds were already occupying two pylons when I arrived. On two nights when there were, respectively, 65 and 51 roosting vultures present, the two species were not evenly distributed between pylons [χ^2 (with Yates' correction) = 28.16, 12.63, both $P < 0.001$]. Instead, most Turkey Vultures roosted on one pylon and most Black Vultures on the other. On the third evening only 10 birds were present, and the distribution of species between pylons did not differ from random (Fisher exact test, $P > 0.05$). Overall, on the three nights that vultures used two pylons, only 1 of 57 Turkey Vultures roosted on the lower level.

DISCUSSION

Vultures did not distribute themselves randomly on the pylons. Instead, when there was little competition for space, most roosted on the upper middle section of the pylon. However, when large numbers of vultures were present, proportionately more Turkey Vultures than Black Vultures roosted on the lower level. Turkey Vultures are less aggressive than Black Vultures and generally subordinate in aggressive interactions at carcasses (Stewart 1978, Wallace and Temple 1987, Houston 1988, Buckley 1996). The observed difference between the species in roosting position when large numbers of birds were present on the pylons is most likely a consequence of the relative aggressiveness of the two species.

The two most likely reasons why the upper level is preferred are that birds on the upper level experience some thermoregulatory benefit or they do not have to endure a rain of droppings from above. Individual vultures probably suffer less heat loss when the upper level is crowded and the birds are pressed close together. Whether such energy savings are a cause or a consequence of communal roosting in vultures is unclear. However, it is known that vultures attempt to conserve energy while roosting. For example, roosting Turkey Vultures allow their body temperature to fall by up to 4° C at night (Heath 1962) to reduce heat loss. The spatial arrangement of branches in tree roosts usually results in vultures being widely separated and limits any thermoregulatory benefits. However, the simple structure of electricity pylons probably promotes energy savings because it presses the birds together in a limited space.

Birds roosting on the lower level of the pylons had to tolerate the droppings of birds roosting above them, but appeared to gain no ameliorating thermoregulatory benefit because they did not crowd together. Thus, birds roosting on the lower level appeared to suffer a cost by doing so. They could have moved to the upper level of an adjacent pylon, but they did not, which suggests they were reluctant to roost alone. This impression is reinforced by the distribution between roosts of Turkey Vultures when two pylons were occupied. On those evenings, the two species segregated between pylons and all but one Turkey Vulture roosted on the upper level. The most likely reason Turkey Vultures are reluctant to roost alone is predation. Reports of predation or attempted predation on vultures are rare (Cole-

man and Fraser 1986, Stolen 1996), but the potential risk from predators such as Barred Owls (*Strix varia*) and Great Horned Owls (*Bubo virginianus*), both of which occur on the refuge, may be sufficient that individual Turkey Vultures are reluctant to roost alone. Those Turkey Vultures that are compelled to roost on the lower level of pylons seem to be making the best choice available to them. Roosting on the lower level of a pylon is not the preferred choice, but is a more attractive option than roosting alone.

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Records of Communal Roosting in Mariana Crows

Gary J. Wiles[1]

ABSTRACT.—Communal roosting is reported for the first time in Mariana Crows (*Corvus kubaryi*) on Guam, Mariana Islands. Counts of at least 66 and 25 birds were made at a roost over a 2-week period. The causes of this behavior are uncertain, but are perhaps related to encounters with brown tree snakes (*Boiga irregularis*), which recently became established on the island. *Received 8 January 1997, accepted 8 September 1997.*

The Mariana Crow (*Corvus kubaryi*) is endemic to Guam and Rota in the Mariana Islands and is the only corvid occurring in Micronesia (Baker 1951). The population on Guam is now restricted to the northern end of the island and is critically endangered, with numbers decreasing from an estimated 350 birds in 1981 to fewer than 20 birds in 1996 (Engbring and Ramsey 1984; Wiles et al. 1995; C. F. Aguon, unpubl. data). The population has declined because of predation by the brown tree snake (*Boiga irregularis*), which invaded the island after World War II (Savidge 1987, Engbring and Fritts 1988). Rota's population of crows also appears to be in decline, falling from estimated 1300 birds in 1982 (Engbring et al. 1986) to a current population of about 600 birds (Grout et al. 1996, National Research Council 1997). Reasons for this decrease are poorly understood, but likely include habitat modification and fragmentation (National Research Council 1997).

Detailed observations of the social behavior of *C. kubaryi* are lacking. Typically, the species is found throughout the year in parties of 2–5 birds, which probably represent family units (Baker 1951; Jenkins 1983; Engbring et al. 1986; Tomback 1986; Michael 1987; C. F. Aguon, pers. comm.). During the 1980s, flocks of 5–15 individuals were also commonly seen flying long distances over the forest canopy and along clifflines on Guam (R. E. Beck, Jr., pers. comm.). These groups were usually temporary, probably consisting of unmated crows and one or more family groups (Michael 1987; R. E. Beck, Jr., pers. comm.). Similar flocks are seen on Rota and very rarely may contain up to 26 birds (E. M. Taisacan, pers. comm.). Larger aggregations have not been reported. This paper documents previously undescribed behavior in *C. kubaryi*—that of communal roosting where large numbers of birds gather at a single location to spend the night.

On 24 February 1984 at 06:56, from a clifftop overlook above the Tarague basin in northern Guam (13° 36′ N, 144° 54′ E), I observed an aggregation of at least 66 crows roosting in several trees below me near the base of the cliffline. The birds were clumped fairly tightly, with the largest concentration consisting of about 35 birds in two dead trees. The crows sat about 30–50 cm apart on the bare branches of both trees. In several nearby living trees, an additional 31 birds were recorded. A few more crows were likely present but hidden from sight by dense foliage. None of the trees were identified to species, but most were slightly emergent above the surrounding forest canopy. I departed from the site at 07:30 with most of the birds still occupying the same trees. The number of crows in the roost represented about 20% of the 1981 population estimate for the island.

The roost was revisited on 9 March 1984 at 06:40, the only occasion that follow-up observations were made. This time, only 25 crows were counted, with 20 individuals in the crown of one tree and five other birds spread among several adjacent trees. Again, a few more birds may have been hidden in the foliage. The roost trees were different from those used two weeks earlier, but were located nearby. All were alive and of similar height to those occupied in February. Other aspects of behavior at the roost (i.e., arrival and de-

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parture times, interactions among birds) were not recorded on either visit.

A number of early morning visits to the site were made in late 1984 and 1985 by other staff of the Division of Aquatic and Wildlife Resources. They regularly saw smaller numbers of up to 10–15 crows roosting in the area (R. E. Beck, Jr., pers. comm.), suggesting that some birds were attracted to the location for an extended period of time.

Only one other record of communal roosting in Mariana Crows is known. A local resident from the village of Yigo in northeastern Guam, with whom I had spoken a few months prior to my observations, stated that he too had seen large roosting aggregations of at least several dozen crows on occasion in the past. His observations were presumably made in the 1960s or 1970s, probably no more than 10 years before crows disappeared from that part of the island. Sightings of this type have never been made on Rota (E. M. Taisacan, pers. comm.; M. Lusk, pers. comm.; D. J. Grout, pers. comm.; R. J. Craig, pers. comm.), despite increased observational survey work on the island since the mid-1980s.

Crows and ravens (*Corvus* spp.) are well known for their gregarious social habits and a number of species form communal roosts at night (Goodwin 1986, Madge and Burn 1994). However, communal roosting is absent or rarely documented for most tropical crows, especially forest-dwelling species (Goodwin 1986, Madge and Burn 1994), although this simply may be the result of inadequate study. Neither has the behavior been reported in the Slender-billed Crow (*C. enca*) of the Philippines and Indonesia (R. S. Kennedy, pers. comm.), the closest relative of *C. kubaryi* (Baker 1951). Protection from wind and cold, improved predator detection, proximity to foraging sites, and the exchange of information on food sources are believed to be some of the benefits derived from communal roosting (Eiserer 1984, Ydenberg and Prins 1984, Marzluff et al. 1996).

In other corvids, the tendency to gather at communal roosts is greatest among nonbreeding individuals (Goodwin 1986, Engel et al. 1992). My records of communal roosting in *C. kubaryi* during late February and early March coincide with the latter half of the species' nesting season on Guam (October to May; C. F. Aguon, unpubl. data). Observations of about 20 breeding pairs during seven years of study have shown that nesting birds and adults with newly fledged young do not leave their nesting territories in the evening (C. F. Aguon, pers. comm.). This suggests that individuals joining large roosts were most likely immatures or adults that failed to breed. Flocking, apparently non-territorial northern Guam crows were regularly seen in the 1980s (R. E. Beck, Jr., pers. comm).

Communal roosting by Mariana Crows is a rare behavior on Guam, at least during the last few decades. It is unknown whether this behavior occurred before the 1960s when the species was considerably more common. If it did not, as evidenced by the absence of earlier reports by island residents, then this may argue that communal roosting is a recent behavioral response to the presence of brown tree snakes. Nighttime encounters with snakes may have stimulated some crows to assemble in nocturnal roosts. Snake densities were high in the vicinity of the Tarague basin at the time of my observations (Rodda et al. 1992). Snakes had probably begun to invade the Yigo area by the late 1960s and were well established there by the 1970s (Savidge 1987). The use of several dead trees by birds at the Tarague roost may have enhanced their ability to detect snakes. Another possibility is that snake predation on nesting crows resulted in greater female mortality and a sex ratio skewed toward males, thereby freeing unmated males to aggregate in large roosts. Brown tree snakes are absent from Rota, where communal roosting has never been observed. Forest conditions at lower elevations on Rota, where most crows occur (Engbring et al. 1986), are similar to those of northern Guam and would not seem to account for the absence of communal roosts on that island.

There are other explanations based on more typical communal roosts in other crows. One is that Mariana Crows form large roosts to be near strongly localized and ephemeral food sources. Considerable variation in roost size over short periods of time, as seen at the Tarague site, often characterizes roosts of this type (Marzluff et al. 1996). However, *C. kubaryi* is not known to exploit foods with these attributes. Unfortunately, further observations of this behavior will probably never be made

again on Guam unless some recovery of this highly endangered population is achieved.

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Three-striped Warbler (*Basileuterus tristriatus*) "Anting" with a Caterpillar

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ABSTRACT.—Anting behavior is widespread among passerine species but its function is unknown. In typical anting episodes, a bird holds an ant or other object in the bill and rubs it in the plumage. In addition to ants, many other objects have been used for "anting." Here I describe the use of a caterpillar for anting by a tropical warbler, and evaluate four of the hypothesized functions of anting in light of this observation. I suggest that an experimental approach is likely to yield insight into the adaptive significance of anting. *Received 5 May 1997, accepted 27 Oct. 1997.*

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Anting is a poorly understood behavior that has been observed in a wide variety of birds, especially temperate-zone passerine species. During "active anting" a bird holds one or more ants in the bill and rubs them on the feathers or skin, typically near the base of the

remiges or rectrices. "Passive anting" involves a bird with spread wings and tail lying on an ant nest and allowing ants to crawl through the plumage. Several hypotheses concerning the function and adaptive significance of anting behavior in birds have been proposed, including (1) removal of, or defense against ectoparasites (Simmons 1985, Clayton and Vernon 1993), (2) protection against fungal or microbial infection (Ehrlich et al. 1986), (3) to soothe skin irritation during molt (Potter 1970, 1989; Potter and Hauser 1974), and (4) as a method of food preparation by removing unpalatable substances (Judson and Bennett 1992). Additional hypotheses have been proposed (reviewed by Whitaker 1957, Chisholm 1959, Simmons 1966). In addition to using ants, birds have been observed "anting" with millipedes (Clunie 1976), flowers (Dennis 1985), mothballs (Dubois 1969, Clark et al. 1990), fruits (Clayton and Vernon 1993), and many other objects (Chisholm 1959, and references above). Here I report an observation of a tropical warbler performing "active anting" with a lepidopteran larva. To the best of my knowledge, anting with a caterpillar has not been reported previously. Most reports of anting involve passerines, especially in the families Corvidae, Sturnidae, Muscicapidae, and Emberizidae. Surprisingly few warblers (Parulinae) have been observed anting (Dater 1953, Tedards 1967), and this is the first report of a tropical paruline anting.

On 20 July 1991, at 07:30, I observed a Three-striped Warbler (*Basileuterus tristriatus*) foraging with a mixed-species flock on the edge of a treefall gap in the Monteverde Cloud Forest Reserve, Puntarenas, Costa Rica. The flock, which included another adult and one immature Three-striped Warbler, was near the intersection of the Chomogo and Pantanoso trails in lower montane rain forest at 1600 m elevation. The warbler captured a large (6 cm long) light green caterpillar and immediately dove from its perch down about 3 m to another perch in the same tree. The bird partially extended one wing at a time, and rapidly rubbed the caterpillar back and forth for about 2 seconds on the underside of each wing near the bases of the first few primary and secondary feathers in the bend of the wing. During the sequence of anting each wing was done twice, the right wing was rubbed before the left wing both times, and the same place was rubbed on each wing. The caterpillar was vigorously writhing in the bird's bill. After anting the bird flew down to a lower perch where it was lost from sight but emerged a few seconds later and spent nearly 20 seconds wiping its bill on the perch. This bill wiping was more exaggerated than is typical for insectivorous passerines (pers. obs.) and included the commisural, loral, and malar regions. Then the bird flew to another small tree where it captured and ate a mottled gray caterpillar that was much smaller and thinner than the first one. It handled this second prey item in a more typical fashion; striking the caterpillar against the branch several times while holding the prey in its bill. I searched the area where the bird disappeared from view but was unable to find the first caterpillar, whose color, size and shape suggested the family Sphingidae (sphinx moth). It is doubtful, however, that the bird had time to consume such a large item in the time it was out of sight.

Most observations of active anting involve pungent substances (Ehrlich et al. 1986, Clark et al. 1990, but see Hailman 1960), and it is likely that the caterpillar also released such a substance because lepidopteran larvae often do so (DeVries 1987). For example, the larvae of the Silver-spotted Sphinx Moth (*Callioniara falcifera*), which occurs in Monteverde and fits the description of the larvae I observed, secrete a bitter yellow substance from a gland behind the head (Haber and Frankie 1980). This substance is thought to contain alkaloids but has not been analyzed. Larvae of the Papilionidae have eversible scent glands (osmeteria) that are believed to contain defensive compounds against predators and parasitoids (DeVries 1980). Additionally, it is well known that many lepidopteran larvae sequester plant compounds making them less palatable prey items (Dyer 1995). Many lepidopteran larvae regurgitate when handled by a potential predator, and such egesta would contain whatever chemicals were in the plant it had been feeding on (L. Brower, pers. comm.).

Because the warbler was foraging when it captured the caterpillar, and because caterpillars are a major component of the diet of *B. tristriatus* (pers. obs.), one might conclude that this observation supports the food prep-

aration hypothesis. Indeed, my first impression was that the bird was attempting to eat the caterpillar. Anting, however, is not the typical method of "food preparation" by *B. tristriatus,* but rather prey items are usually hit against the branch as this bird did with the second caterpillar. On the other hand, anting may be the typical food preparation of toxic prey with banging the typical preparation for nontoxic prey.

The molt irritation hypothesis is a possible explanation, considering that molt is usually symmetrical and this bird anted in the same place on both wings. *Basileuterus tristriatus* molts its primaries and secondaries sometime between early June and early August (F. G. Stiles, pers. comm.). I looked for, but could not see any signs of molt; however, it would be difficult to determine on a free-ranging small bird. Defense against ectoparasites or fungal infections is also possible although uncertain because I was unable to identify the caterpillar or examine the bird. It is interesting that so few tropical birds have been observed anting (Skutch 1948, Sutton 1951, Sick 1957, Whittaker 1996) as one might expect fungal or microbial infections to be at least as common in the humid tropics as in the north temperate zone. Skutch (1996:70), however, implies that he has seen anting behavior many times in Central America and notes that anting in the tropics usually takes place in trees or shrubs, whereas anting usually occurs on the ground in the temperate zone. Perhaps for this reason, many instances of anting in the tropics go unobserved.

Anting remains one of the unexplained puzzles of ornithology. The available information is dominated by anecdotal observations (such as this one). The diversity of items used for anting suggests that it is an opportunistic behavior induced by some feature of the ant or other object used. An experimental approach is likely to shed light on the function(s) of anting, but the few experiments thus far have reached conflicting conclusions (Judson and Bennett 1992, Clayton and Vernon 1993, Clayton and Wolfe 1993) perhaps because each has tested only one of the hypothesized functions.

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Adoption Of Yellow Warbler Nestlings By Song Sparrows

G. A. Lozano[1,2] and R. E. Lemon[1]

ABSTRACT.—Although interspecific brood adoption has been reported in several species of birds, the process by which it occurs has seldom been reported. We observed a pair of Song Sparrows (*Melospiza melodia*) that adopted a brood of Yellow Warblers (*Dendroica petechia*) and, gradually, over several days, took over the parental duties of the original parents. During the first five days of the nestling period, the brood was only attended by Yellow Warblers. In the following three days, however, a pair of Song Sparrows took over an increasingly larger proportion of the parental duties. This adoption probably resulted from misdirected parental care. Although the factors that led to the adoption are unknown, it is clear that the absence of the original parents was not prerequisite. *Received 30 June 1997, accepted 3 Oct. 1997.*

Interspecific parental care has been reported for several species of birds (e.g., Southern 1952, Watson et al. 1993). Perhaps the best known example is that of a Northern Cardinal (*Cardinalis cardinalis*) feeding a group of goldfish at the edge of a pond (Welty 1982). These accounts are usually limited to the actual observation of young of one species being cared by parents of another, and provide no information about the process by which this situation arose. Here we report an instance of adoption of Yellow Warbler (*Dendroica petechia*) nestlings by a pair of adult Song Sparrows (*Melospiza melodia*), and document a gradual process whereby over a period of a few days the Song Sparrows took over the parental duties of the original Yellow Warbler parents.

Our observations were obtained as part of a study of parental behavior in Yellow Warblers (see Lozano and Lemon 1996 for further details about the methods). During June 1995, at Pointe a Fourneau (45° 55′ N, 73° 51′ W), Île Perrot, Quebec, Canada, we were conducting focal nest watches of several nests of a population of Yellow Warblers. The nest in question had been built in late May; the first egg was laid on May 29, and 4 additional eggs were laid on consecutive days. Of these eggs only 4 hatched, but, as part of an experiment, the brood size at this nest was increased to 6 nestlings. Two other nestlings of similar age and size were obtained from other Yellow Warbler nests, and were added the day after the nest's first nestling hatched.

Nest watches lasted 30 min and were conducted daily from the time nestlings were 3 days old until fledging occurred. During the first 3 nest watches only the two Yellow Warbler parents visited the nest (Fig. 1). In addition to feeding the nestlings, the female brooded them for 2:15, 0:45 and 11:40 min:s respectively. During the fourth watch, when the nestlings were 6 days old, a Song Sparrow fed the Yellow Warbler nestlings, as did the two Yellow Warblers parents. The two species were never present at the nest at the same time.

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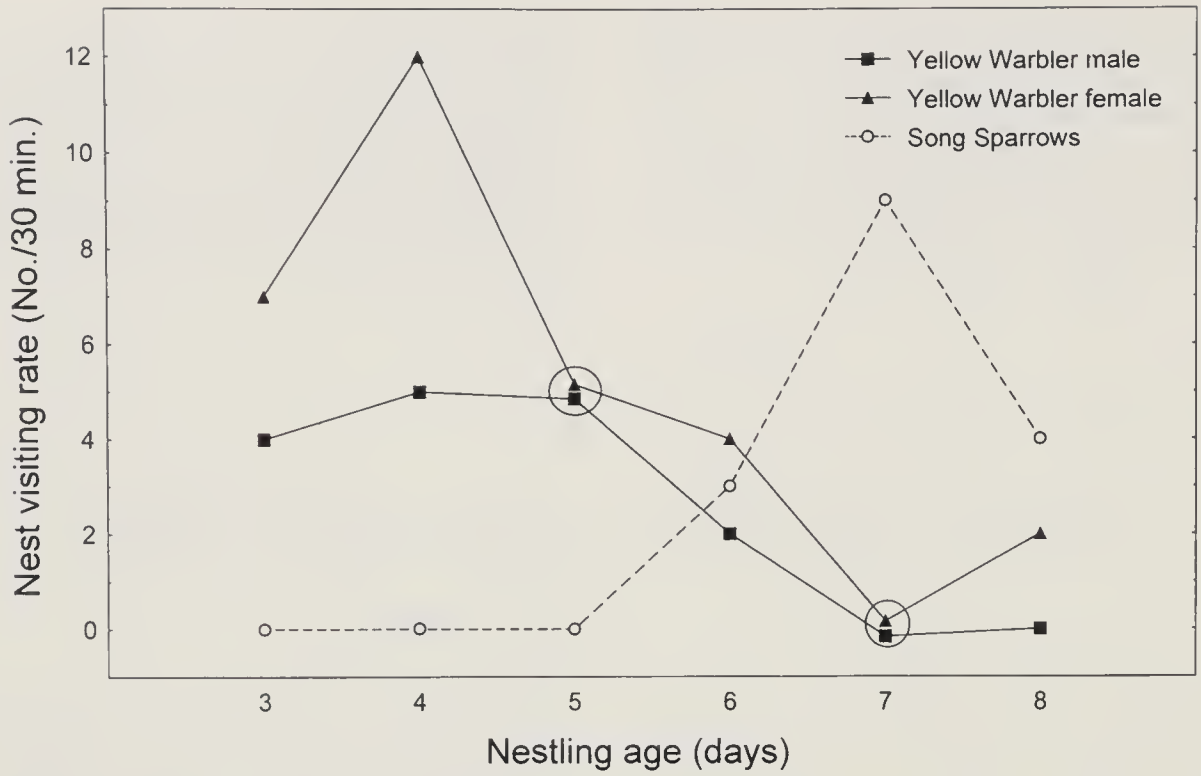

FIG. 1. Nest-visiting rates of Yellow Warbler and Song Sparrows. Circled data points have the same values, and are separated only for graphical purposes.

The next day the male Yellow Warbler was not seen. The two sparrows chirped defensively at us when we approached the area, and at a Gray Catbird (*Dumetella carolinensis*) that happened to approach while we were observing the nest. Although the parental contributions by the pair of sparrows was not differentiated by sex, both birds were feeding the nestlings and removing fecal sacs. When the nestlings were 8 days old both Yellow Warblers were seen in the territory, often perched nearby, but only the female approached the nest. The two sparrows made most of the feeding trips during the observation period (Fig. 1). We did not observe any apparent signs of aggression between the two species. Finally, the next day the nest was empty, presumably because the nestlings had fledged. Although parental care does continue after fledging, it is seldom observed because it is very cryptic and does not occur at any specific place. Neither the nestlings nor their parents, natural or foster, were seen again.

Although adaptive explanations have been sought to explain instances of intra-specific adoption (e.g., Gori et al. 1996), most of these are not applicable in this case. Perhaps the only exception is the recent suggestion that helping behavior is the result of individuals attempting to gain "prestige" by demonstrating their ability to rear offspring (Zahavi 1995). Although this idea was developed to explain intraspecific helping behavior, it could also be applied to inter-specific cases of brood adoption. Nonetheless, the behavior we observed was most likely the result of misdirected parental behavior. If there is a cost associated with providing parental care, the Yellow Warbler parents may have actually benefited from this error. We do not know the fate of the original sparrow nest, or even if there ever was one, so we do not know the factors that precipitated the adoption. However, it is clear that the absence of the original Yellow Warbler parents was not a prerequisite for this adoption.

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Evident Nest-Searching Behavior of Female Brown-headed Cowbirds While Attended by Males

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ABSTRACT.—Unlike most birds, brood parasitic Brown-headed Cowbirds (*Molothrus ater*) must find host nests in which to lay their eggs. Female cowbirds have been reported using several methods to find nests. Here, I report on two observations of cowbirds near host nests that are consistent with two hypotheses, nesting-cue and "flush" method, regarding techniques cowbirds may use to find host nests. The nesting-cue hypothesis poses that cowbirds are directed to host nests by host's typically increasing aggressive behavior towards cowbirds as they approach the nest, whereas the flush method poses that cowbirds attempt to spot a concealed nest by rousing the host from it with intentionally noisy behavior near the nest. Unlike other reported observations of female cowbirds near potential host nests, male cowbirds were present during both observations. *Received 20 June 1997, accepted 27 Oct. 1997.*

Brown-headed Cowbirds (*Molothrus ater*) are obligate brood parasites that lay their eggs in the nests of other species, the 'hosts'. Norman and Robertson (1975) summarized three main methods female cowbirds use to find host nests: (1) secretive searching while walking; (2) active, noisy searching; and (3) cryptic, silent watching of nest-building hosts (Hann 1937, 1941; Norris 1947; Mayfield 1960, 1961; Payne 1977). While conducting field work at The Morton Arboretum in Lisle, Illinois, I observed what appeared to be all three of these methods. While cryptic watching of host nest-building has been well documented, other methods have rarely been described (Norman and Robertson 1975). Further, previous studies either state or imply that female cowbirds search for and approach host nests when alone (i.e., Friedmann 1929; Hann 1937, 1941; Norris 1947; Norman and Robertson 1975). Here, I report on my observations of female cowbirds seemingly searching (e.g., the flush method) for host nests by using conspicuously noisy searching and host nest defense that has not been previously described.

Seppä (1969) and Ficken (1961) first suggested that the European Cuckoo (*Cuculus canorus*) and cowbird, respectively, may use host nest-defense to locate nests. Robertson and Norman (1976) later proposed the "nesting-cue" hypothesis which poses that brood parasites take advantage of host nest defense to direct them to the nest. However, this behavior has never been observed in cowbirds.

Many species of birds react aggressively toward cowbirds (e.g., Robertson and Norman 1976, 1977; Folkers 1982; Smith et al. 1984; Folkers and Lowther 1985; Neudorf and Sealy 1992; Bazin and Sealy 1993; Peer and Bollinger 1997). Nest defense may be an effective deterrent to parasitism (Slack 1976) for relatively large host species (Friedmann 1929, Neudorf and Sealy 1992), as they can inflict injury on cowbirds (Leathers 1956). However, nest defense may be ineffective, especially for smaller host species and those less equipped

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to defend their nests (Robertson and Norman 1977, Montgomerie and Weatherhead 1988). For species unable to prevent parasitism, it is unclear why some species act aggressively towards cowbirds, as the action may help direct cowbirds to their nest. It has been suggested that nest defense by such hosts may be an instance of a more general response to all potential enemies that approach the nest (Robertson and Norman 1976, Smith et al. 1984), although more recent studies have shown that some host species recognize the unique threat posed by cowbirds (Neudorf and Sealy 1992, Bazin and Sealy 1993, Gill and Sealy 1996). Cowbirds may be more likely to use host nest-defense to find nests when the host species is small and less likely to injure the cowbird.

Evidence that nesting-cues could potentially be used by cowbirds was provided by Uyehara and Narins (1995) and Gill and coworkers (1997), who found that some host defensive responses toward live cowbirds and models, respectively, increased with decreasing distance from the nest. In addition, Smith and coworkers (1984) found that the level of parasitism was positively correlated with the level of nest defense in Song Sparrows (*Melospiza melodia*). However, studying six different species, Gill and coworkers (1997) did not find a positive correlation, and they concluded that nest defense was unlikely to be used as a nest-locating cue by cowbirds. My observation of interactions between a female cowbird and nesting Field Sparrows (*Spizella pusilla*) is consistent with the nesting-cue hypothesis.

While monitoring a Field Sparrow nest in its third day of incubation, I observed a female cowbird, attended by two males, approach the nest. The incident occurred on 6 June 1996 at 11:10 CST when the pair of sparrows, perched within 2 m of their nest, began calling in response to a female cowbird that landed approximately 10 m away. As the female cowbird made short flights in their direction, the sparrows began to flit around the area of the nest and call more frequently. When the cowbird was approximately 1 m from the nest, the sparrows' calling and flitting became more frequent for approximately 30 s while the cowbird walked and hopped through the vegetation near the nest. When the cowbird was within 0.5 m of the nest, the sparrows began striking her repeatedly for several seconds until she reached the nest. She then immediately flew off, followed by the two male cowbirds. The cowbird did not defend herself. Although the male cowbirds never approached the nest, one remained within approximately 8 m of the female for the duration of her search. While the nesting-cue hypothesis poses that cowbirds use host nest defense to find nests to parasitize, the nest was never parasitized. This may be because the nest's completed clutch of four eggs indicated that the nest was in the incubation stage making it poorly suited for parasitism. Cowbird eggs laid in host nests undergoing incubation often do not hatch or hatch too late to compete successfully (Weatherhead 1989, Robinson et al. 1995). All four sparrow eggs eventually fledged young.

I also observed behavior similar to that described by Wiley (1988) and Norman and Robertson (1975), studying the Shiny Cowbird (*M. bonariensis*) and Brown-headed Cowbird, respectively, in which they described cowbirds seemingly attempting to flush a nesting bird from hiding. On 13 May 1997 at 11:45 CST I spotted a female cowbird flying in a "hovering" fashion less than 1 m above 15 cm tall grass. The cowbird appeared to be searching as her neck was extended and head pointed down. She continued to fly in a slow circular motion, occasionally dropping with her wings outstretched causing them to contact the grass. After a few seconds on the ground, where she would walk without feeding, she would flit up and repeat the process approximately 20 cm away. All of her "hovering" and walking activities took place within a 2 × 2 m area. After 2 min, a male cowbird landed approximately 3 m away and called. I then spotted an approaching Song Sparrow issuing alarm 'tchunk' calls (Nice 1937) in flight approximately 15 m away. The sparrow flew directly towards the female cowbird who immediately flew away, followed by the male cowbird. The sparrow never got closer than 1 m from the cowbird. It is unlikely that the returning sparrow was off the nest as a result of being flushed by the cowbird, because the sparrow would likely have initiated nest defense immediately instead of departing for two minutes. Upon searching the area, I found a Song Sparrow nest with four cool sparrow eggs and two cowbird eggs within 0.5

m of where the cowbird had been walking and hovering prior to her retreat. The nest was under a tuft of dead grass and was not visible from directly above. The following morning a sparrow egg had been removed and a third cowbird egg was present, all of which were being incubated.

The benefits to cowbirds of using the flush method for finding host nests are unclear, because that method is most effective during the host's incubation stage when freshly laid cowbird eggs have a low chance for success. However, the flush method may be adaptive when a host is on the nest during egg laying or when incubation begins prior to host clutch completion.

In conclusion, unlike other studies, both of my observations confirm that male cowbirds may sometimes accompany females at host nests. Further, I witnessed a female cowbird behaving similarly to the behavior described by Norman and Robertson (1975), who hypothesized that the behavior's purpose might be to flush a bird from hiding. Finally, consistent with the nesting-cue hypothesis, I observed host defensive behaviors escalate as a female cowbird approached and found the hosts' nest. It is notable that in this observation the host species, Field Sparrow, is approximately one-third the size of a cowbird (Dunning 1993). Further work on the nesting-cue hypothesis should examine the effect of host size on cowbird employment of this search method.

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Characteristics of Florida Grasshopper Sparrow Nests

Michael F. Delany[1,2] and Stephen B. Linda[1]

ABSTRACT.—We examined nests of the endangered Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) on the U.S. Air Force Avon Park Range, Highlands County, Florida. Nests (n = 20) were located on the ground in shallow (≤3.2 cm) excavations in the sand substrate. All were domed (>50% of the cup covered) and made of grass and grass-like monocots. Most (75%) were shielded by a low (<29.5 cm) growth of dwarf live oak (*Quercus minima*). Nest opening directions were randomly oriented ($P > 0.05$). Vegetation density was significantly lower in the nest opening quadrant than in other quadrants ($P = 0.003$). An exposed area at the nest opening would facilitate access and make predator distraction displays more visible. *Received 24 May 1997, accepted 4 Oct. 1997.*

The Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) is an endangered subspecies endemic to the south-central prairie region of the state (Fed. Reg. 1986). Basic information on nesting ecology is needed to develop and implement conservation strategies for the sparrow (USFWS 1988). Nest location, structure, and orientation may have important implications for reproductive success and population stability. Previous descriptions have been anecdotal (Howell 1932, Nicholson 1936). In this paper we present data on the placement, composition, dimensions, and orientation of Florida Grasshopper Sparrow nests.

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STUDY AREA AND METHODS

Data were collected during 20 May 1993–31 July 1996 on the U.S. Air Force Avon Park Range, Highlands County, Florida. The study area was a 700 ha grass, shrub, and saw palmetto (*Serenoa repens*) plant community described by Delany et al. (1985). The prairie was burned with head fires (burned with the wind) between December and mid-March on a 2–3 year rotation.

The study area was systematically searched by walking transects at 50 m intervals. Observations of Grasshopper Sparrows delivering food to nestlings and females flushed from nests indicated possible nest sites. Nests were found by searching these locations. After termination of the nesting attempt, we measured nest outside diameter, nest inside diameter, nest height above substrate, and orifice width (diameter of the nest opening). Orientation of the nest opening was measured with a compass and grouped in 90° quadrants centered to orientations N, S, E, and W. Nests were measured in place within 5 days of termination.

Features of the vegetation composition and structure were measured at each nest in the 4 cardinal directions. Point subsample measurements (4/nest) were made within 1 cm of the nest and included: (1) vertical density—the total number of vegetation contacts with a 7 mm diameter metal rod placed vertically into the vegetation; (2) height—the height of the highest contact with the rod; and (3) percentage cover—the total cover by each of the vegetation components (grasses, forbs, shrubs, litter, and bare ground) as determined by counting the number of cm of each component along a 1 m transect adjacent to point samples (Whitmore 1981). Plant species providing shielding to the nest were recorded. Time post-burn was recorded for all sample locations.

Fifteen nests were collected and plant species used in construction were identified, and their relative abundance was visually estimated. Plant names follow Wunderlin (1982).

To test the null hypothesis that nest opening direction was uniformly distributed against any alternative

TABLE 1. Plant species (≥ 20% occurrence) comprising Florida Grasshopper Sparrow nests (n = 15), Avon Park Air Force Range, Highlands County, Florida, 20 May 1993–31 July 1996.

Plant species	% occurrence
Elliot's yellow-eyed grass (*Xyris elliottii*)*	87
Roadgrass (*Eleocharis baldwinii*)*	87
Wiregrass (*Aristida beyrichiana*)	80
Bluestem (*Andropogon* sp.)	80
Short-leaf yellow-eyed grass (*Xyris brevifolia*)	73
Yellow hatpins (*Syngonanthus flavidulus*)	60
Dwarf live oak (*Quercus minima*)	47
Panic grass (*Dicantheleium ensifolium*)	47
Moss (*Polytrichum* sp.)	33
Golden aster (*Pityopsis graminifolia*)	27
Torrey's nutrush (*Scleria reticularis*)	27
Bottlebrush threeawn (*Aristida spiciformis*)	20

* Species that comprised a distinct inner lining of the nest cup.

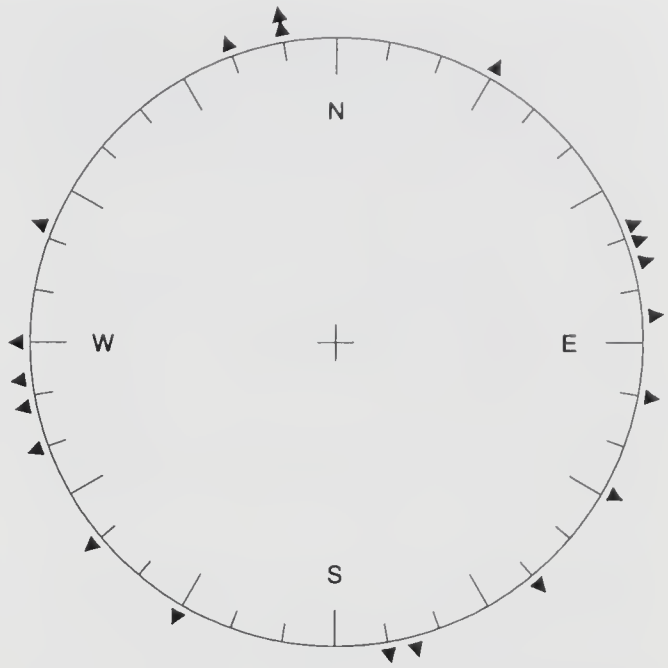

FIG. 1. Orientation of nest entrances of 20 Florida Grasshopper Sparrow nests at Avon Park Air Force Range, Florida. Triangles show direction of opening. Opening directions were randomly oriented ($P > 0.05$).

hypothesis, the omnibus test (Fisher 1993) was performed, in which the modified Kuiper statistic (V) was computed. A Rayleigh test (Fisher 1993) was performed to test the null hypothesis of uniformity against unimodal and bipolar alternatives.

An analysis of variance (ANOVA) was performed to test for differences in percent bare ground coverage and density (number of vegetation contacts) between the compass quadrant towards which a nest opened and other quadrants. In order to induce homogeneity of variance, the Box-Cox variance stabilizing transformation for vegetation contacts was used. The logit transformation was used for percent bare ground to maintain consistency with Aitchison's (1986) approach for the analysis of compositional data. The 0% bare ground value in the dataset was changed to 1% bare ground for this analysis because the logit of 0% is $-\infty$. A split-plot model was used in the ANOVA, in which the main-plot factor was MONTHS POST-BURN, the main-plot error term was NEST NUMBER WITHIN MONTHS POST-BURN, the sub-plot factor was QUADRANT (levels were: nest opening quadrant and not nest opening quadrant), and the sub-plot error term was QUADRANT × NESTNUMBER WITHIN MONTHS POST-BURN. If the MONTHS POST-BURN × QUADRANT interaction was not significant, then that term was deleted from the model, the reduced model was fitted, and the reported P-value for QUADRANT was based on the reduced model. Least-squares means for QUADRANT levels were back transformed to the original scale, and the SE of the back transformed least-squares means was obtained by application of the delta method.

RESULTS

Twenty active nests (containing eggs or young) were located on the ground in shallow (≤3.2 cm) excavations in the sand substrate. Nest cup rims were level with or slightly (≤1.3 cm) above the ground. Primary shielding vegetation was dwarf live oak (*Quercus minima*, n = 15), but also included wire grass (*Aristida* sp., N = 1), gopher apple (*Licania michauxii*, n = 1), yellow-eyed grass (*Xyris* sp., n = 1), saw palmetto (n = 1), and St. Johns-wort (*Hypericum brachyphyllum*, n = 1).

Nest material was a mixture of several narrow leaved grasses and grass-like monocots (Table 1). Nests (n = 15) were comprised mainly of wire grass, bluestems (*Andropogon* sp.), and yellow-eyed grass (*Xyris* spp.). Mean nest outside diameter was 10.3 cm (SD = 0.9, range = 8.8–12.3), inside diameter was 6.9 cm (SD = 0.6, range = 5.8–7.9), and height was 7.7 cm (SD = 0.5, range = 6.5–8.5). All nests were domed (nest material covered ≥50% of the cup) with an average orifice width of 5.1 cm (SD = 0.8, range = 3.7–7.2). Opening directions were randomly oriented (V = 0.88, $P > 0.05$; Fig. 1) and not significantly grouped using unimodal and bipolar alternatives ($P > 0.05$ for each test).

Nests were located in grasslands that were 4 (n = 16), 16 (n = 1), and 24 months (n = 3) post-burn. Differences in bare ground coverage and vegetation density at the nest site were evident after fire (Table 2); however, the

TABLE 2. ANOVA results of a comparison of bare ground coverage and vegetation density (number of contacts) in the compass quadrant towards which a nest opened with the same features in other quadrants (n = 20 nests). Results are for reduced model (P-values for MONTHS POST-BURN × QUADRANT were 0.68 and 0.28 for % bare ground and CONTACTS, respectively). Avon Park Air Force Range, Highlands County, Florida, April 1993–July 1996.

Response variable	Source	df	Type III mean square	F	P-value
$\log\left(\frac{\text{percent bare ground}}{\text{100-percent bare ground}}\right)$	Months POST-BURN	2	9.4899	14.47	0.0002
	Quadrant	1	0.1090	0.25	0.6211
log (CONTACTS + 1)	Months POST-BURN	2	2.8967	3.37	0.0586
	QUADRANT	1	5.6966	11.71	0.0029

quadrant effect did not depend on months post-burn for either response variable (P > 0.05 for each). The back transformed least squares mean bare ground coverage in the nest opening quadrant ($\hat{\bar{x}}$ = 21.2, $\widehat{SE}$ = 4.3) was higher than in other quadrants ($\hat{\bar{x}}$ = 16.9, $\widehat{SE}$ = 2.1) but the effect was not significant (P = 0.05; Table 2). However, the mean number of vegetation contacts in the nest opening quadrant ($\hat{\bar{x}}$ = 4.1, $\widehat{SE}$ = 1.1) was significantly lower (P = 0.003) than in other quadrants ($\hat{\bar{x}}$ = 12.8, $\widehat{SE}$ = 2.0).

DISCUSSION

The placement, dimensions, and composition of Florida Grasshopper Sparrow nests were similar to those reported for other subspecies (McNair 1984, Vickery 1996). However, most (75%) *A. s. floridanus* nests were shielded by dwarfed shrubs rather than grass clumps (sources cited above). Unpublished information from Florida Grasshopper Sparrow oological collections (McNair 1986) indicated that 28 of 44 nests were shielded by saw palmetto (D. B. McNair, pers. comm.). Compared to the eastern race (*A. s. pratensis*), habitat occupied by *A. s. floridanus* had a much higher value for shrub cover (including saw palmetto; Delany et al. 1985) which appears to be the preferred nesting site.

Wiens (1969) reported a nonrandom east and northeast orientation of most (10 of 15) Grasshopper Sparrow (*A. s. pratensis*) nest openings in Wisconsin. Nonrandom nest orientation of some grassland birds has been related to thermal constraints (With and Webb 1993). In our study, orientation may have been random because openings were positioned towards areas of low vegetation density and bare ground near nests. Results were consistent despite significant differences in vegetation structure related to time post-burn. Adults visiting a nest usually approached the entrance on the ground (pers. obs.). Also, adult females flushed from nests engaged in predator distraction displays (see Vickery 1996). An exposed area near the nest entrance would facilitate access and make distraction displays more visible.

Grasshopper Sparrows are ground-dwelling birds that usually require at least 20% bare ground for unrestricted movement but enough vegetation to provide nest cover (Whitmore 1981, Vickery 1996). Frequent burning maintains prairie grasslands in a sparse, early successional stage (Delany et al. 1985) and appears to provide vegetation compositions suitable for nesting at this location. Features of occupied and abandoned territories indicate the Florida subspecies probably cannot adapt to habitat perturbations that remove potential nest sites (Delany and Linda 1994). Information presented here provides a better understanding of the sparrow's habitat requirements. Measures of Florida Grasshopper Sparrow reproductive success are needed to determine habitat quality and evaluate variables influencing nesting outcome. If *A. s. floridanus* continues to decline in numbers and nears extinction, the Recovery Plan (USFWS 1988) recommends that a captive population be established. Information on nests and nest sites of a wild population would be important should that recovery effort become necessary.

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Ornithological Literature

Edited by William E. Davis, Jr.

THE ORIGIN AND EVOLUTION OF BIRDS. By Alan Feduccia. Yale University Press, New Haven, Connecticut. 1996: 420 pages, 470 unnumbered figures. $65.00 (cloth).—This is a remarkable book. Alan Feduccia has compiled an amazing amount of information on the morphology, evolution, systematics, and paleontology of birds. Anyone interested in these topics should own this treatise, which summarizes Feduccia's own studies as well as those of many other ornithologists and paleontologists, but especially Larry D. Martin (Mesozoic birds) and Storrs L. Olson (Cenozoic birds, relationships of modern birds).

The text is accompanied by numerous illustrations and photographs, mostly borrowed from other sources. The ink drawings of birds by George M. Sutton (from Van Tyne and Berger's *Fundamentals of Ornithology*) are familiar and pleasant. The original drawings and paintings by John P. O'Neill are very nice, although that of *Didunculus* on page 249 shows a bird with psittacid rather than columbid head and body proportions, perpetuating the myth that the tooth-billed pigeon of Samoa might be related to parrots. (There also is no evidence, contra Feduccia, that *Didunculus* is closely related to the extinct dodos of the Mascarenes.) The quality of reproduction of the half-tones is mediocre. Numbering the figures would have helped to relate them more precisely to the text. Some legends are confusing. Also, the paper is thin and warps easily.

Nowhere is it said who other than Feduccia read the MS before it was published. A careful review by another ornithologist or paleontologist would have helped to eliminate the many factual errors that are sprinkled through the text and figure legends. While reading Chapters 5–8, for example, I noted such errors on 23 of these 179 pages.

Nevertheless, Feduccia's narrative does a good job of explaining topics never before dealt with outside of the primary literature. Time after time he points out conflicts between the fossil record and molecular clocks, such as in the Oscine-Suboscine dichotomy and the never-ending dilemma of ratite relationships. The strongest parts of the book are Chapters 3–5, titled "Genesis of Avian Flight," "Birds of the Cretaceous," and "Flamingos, Ducks, and Long-legged Waders," where Feduccia presents many original ideas and well formulated explanations.

One of the most important developments in vertebrate paleontology has been the newly discovered diversity of Mesozoic birds. Long gone are the days when Mesozoic birds of any note consisted of *Archaeopteryx, Hesperornis, Ichthyornis,* and little else. Feduccia introduces us to these early birds from China, Mongolia, Spain, Argentina, and elsewhere. The most common group of Mesozoic birds is the Subclass Enantiornithes, characterized by pectoral and tarsal structure that is fundamentally different from that of modern birds. Perhaps even more exciting has been the discovery of birds from both the Early and Late Cretaceous that have an essentially modern flight apparatus. This last group forces one to doubt that the much more reptilian *Archaeopteryx,* in spite of its sophisticated feathers, is on the main line leading to modern birds.

Interpretation of the Mesozoic bird fossils is contentious. Two fundamental issues form the core of the dispute. One is how the various early birds are related to *Archaeopteryx,* to each other, and to living birds. The other, perhaps fueled in part by the public allure with dinosaurs, is whether birds originated from theropod dinosaurs or from some other archosaurs, such as thecodonts or crocodilians. Both concepts of avian origin are backed by some good evidence. The pro-theropod camp is dominated by scientists who, unlike Feduccia, try to adhere strictly to cladistic methodologies. Feduccia points out the difficulties in determining character polarities, in distinguishing phylogenetically genuine similarity from convergence or homoplasy, and in the concept of parsimony. The question of bird vs reptile is irrelevant to cladists who regard birds simply to be theropods. This leads to phrases such as "non-avian dinosaur" and

"non-avian theropod," which seem to me to be the conceptual equivalent of "non-reptilian amphibian" or "non-amphibian fish." Feduccia disagrees with the theropod origin of birds and has steadfastly pointed out problems involving chronology, dental morphology, origin of flight, forelimb proportions, homology of the wrist and manus, and homology of the tarsals and metatarsals.

It is much too early to expect a consensus on the origin of birds. Because both sides have evidence to support their views, a more tolerant tone would keep the arguments at a scholarly level. Indelicate reviews of Feduccia's book, such as that by bird-theropod advocates Norell and Chiappe (1996, *Nature* 384:230, entitled "Flight from reason"), do little to sustain the reviewers' own cause. To criticize a paleontologist for relying too much on the fossil record is like faulting a mason for building with bricks.

The controversies over the origin of birds are another example of a non-compromising, black-and-white, winner-take-all argument between opposing camps of systematists. Such debates, often as personal as they are scholarly, cast a dark shadow over the field of avian systematics. The polarization will begin to subside only when the major players admit that progress in understanding the origin, evolution, and relationships of birds can be made by scientists with diverse specialties, whether muscles or molecules, bones or behavior, physiology or fossils. No single person can do it all or even claim to understand it all. Rarely, if ever, can we expect any single set of data to lead us to the promised land. We are interested in progress; the final word may never come. In the meantime, let us enjoy the new discoveries. Feduccia now has compiled more information about the origin and evolution of birds than anyone else. He is to be congratulated for this, regardless of his errors or of his methodological/conceptual differences with others.—DAVID W. STEADMAN.

RED-COCKADED WOODPECKER: RECOVERY, ECOLOGY AND MANAGEMENT. Edited by David L. Kulhavy, Robert G. Hooper, and Ralph Costa. College of Forestry, P.O. Box 6109, Stephen F. Austin State University, Nacogdoches, Texas 75962. 1995: 552 pp., 7 color plates. $54.96 + $4.00 shipping and handling (hardback).—The Red-cockaded Woodpecker [RCW] (*Picoides borealis*) is probably the most studied North American woodpecker and may also qualify for inclusion among the ten most studied bird species in North America. It has received this kind of attention from a wide spectrum of individuals and agencies because its survival has been threatened seriously for many years. It was designated as an endangered species in 1968. This large format volume (22 × 28.5 × 3.75 cm) contains the proceedings of the Third Red-cockaded Woodpecker Symposium held in January 1993 and attended by more than 300 persons. It includes 65 edited papers by 114 authors and coauthors divided into six sections: 1. Outlook for Recovery, 2. Strategy for Recovery, 3. Natural Disturbances, 4. New Insights on the Biology, 5. Cavity Trees as a Resource, and 6. Status. Shorter parts, such as literature cited, subject index, index of scientific names, list of contributors, and short biographical sketches of the editors and photographer complete the book. The papers are carefully edited and include a useful abstract and keywords. The presentation is pleasant and of high quality.

In the first section, M. C. Meier summarizes the processes that have led to what he calls "an emerging success story" toward the recovery of RCW. In another paper R. E. F. Escano describes the population status and management on land administered by USDA Forest Service. J. A. Jackson contributes a history of the knowledge on this woodpecker since its description in 1807 and gives a good overview on the research and interest that it has generated since its designation as an endangered species.

The second section should be of great value to those who are interested in or are responsible for the management and implementation of measures for the recovery of an endangered species. The papers deal with several aspects of management including ecological strategies and use of modern computer techniques. The third section covers aspects of natural disturbances that could affect recovery plans and includes phenomena such as hurricanes and wind damage, beetle infestations, lightning, and forest architecture. A paper entitled "Eco-

nomic valuation of the Red-cockaded Woodpecker and its habitat" provides interesting ideas on "how to assign economic values to goods which are not traded in the market place." Anyone who may have to address this issue or promote a project dealing with the conservation of species or habitats, particularly in the financial and/or political arenas, should read at least this section of the book. The fourth section reviews the results of recent research on various aspects of the biology of RCW, and includes articles on populations, genetics, habitat use, land management, ecology, morphology, and parasites. Section five, deals exclusively with cavity trees and includes papers on artificial cavities, predation, interspecific competition, tree characteristics, and forest composition and structure. In the last section, the status of the RCW is reviewed from different perspectives, each providing an interesting insight on the status of the bird and its future. The bibliographic section is extensive and should be useful to anyone looking for more information than what is given in the papers which, no doubt, had to be reduced to their essential elements.

This well organized book will be useful to anyone dealing with the ecological management and recovery plans for endangered or threatened species although it deals strictly with a single forest species. Many of the principles and procedures described in the papers could be adapted to other situations or serve as examples for management projects. This book should be available to students, teachers, resource managers and planners who will find it a good source of information. Politicians involved in the conservation of natural resources should be required to read and understand crucially important chapters of this book if the endangered and threatened species of the continent are to survive.—HENRI OUELLET.

EAGLE'S PLUME: PRESERVING THE LIFE AND HABITAT OF AMERICA'S BALD EAGLE. By Bruce E. Beans. Scribner, New York, New York. 1996: 318 pp., 20 black-and-white photographs, $25.00 (cloth).—The Bald Eagle (*Haliaeatus leucocephalus*), arguably America's most widely recognized bird, is also one of its most evocative. Dig deeply enough, and almost everyone has an opinion about the National bird. Benjamin Franklin, disgusted by the Continental Congress's choice of the Bald Eagle in 1784 as part of the new nation's national emblem, attacked the species in a now famous letter to his daughter, arguing that the bird's piratical habits precluded its use in such a lofty position. Almost two hundred years later, conservation biologists in Canada and the United States embraced the plight of reproductively constrained, pesticide-laden Bald Eagles in their fight to ban the widespread use of DDT in North America. That Franklin's eloquent arguments fell on deaf ears while those of 20th Century conservationists did not, is testimony to the species' mystical—indeed, almost addictive—appeal. As someone who helps introduce hundreds of Hawk Mountain visitors to southbound Bald Eagles each fall, I am convinced that one could build a religion around the bird. But over the past 50 years Bald Eagles have been the subject of 100s, if not 1000s, of newspaper and magazine articles, and dozens of books. So when all is said and done, do we really need another book about Bald Eagles? Haven't all the bases already been touched? "Eagle's plume" suggests otherwise.

Bruce E. Beans has written not so much another book about Bald Eagles, but rather a book about Bald Eagle conservation, or, more exactly, about Bald Eagle protagonists and antagonists. This is not to say that the book doesn't deal with the eagles themselves. It does, and for the most part eagle ecology is presented in both a credible and readable manner. But the real heart of the book—and what will be of particular interest to Wilson Society readers—is its description of the many personalities involved in Bald Eagle conservation. Included are descriptions of the actions of many past or present Wilson Society members and associates, including detailed accounts of such "Bald Eagle luminaries" as Charles Broley, Larry Niles, and Mitchell Byrd. Also included are many of the enemies Bald Eagles have faced over the years, human and otherwise.

Although the book wanders a bit in its concluding chapters, most of the work provides a well-researched history of the species' trials

and tribulations through the DDT-Era of the 1950s, 60s, and 70s, into the Coastal Development Era of the 1980s and 90s. While specialists in the field might quibble with the author's emphases, the book's engaging and well-documented prose compares favorably with Jonathan Weiner's critically acclaimed "The beak of the finch." I strongly recommend "Eagle's plume." The next time someone asks you what conservation biologists are like, tell them to read this book.—KEITH L. BILDSTEIN.

NEOTROPICAL MIGRATORY BIRDS: NATURAL HISTORY, DISTRIBUTION, AND POPULATION CHANGE. By Richard M. DeGraaf and John H. Rappole. Comstock Publishing Associates, Ithaca, New York. 1995: 676 pp., 361 range maps, 2 appendices. $27.50 (paper).—This reference book briefly treats each of 361 species of Neotropical migrants, providing a range map, range description, summary of the conservation status of the species, habitat description, special habitat requirements, and selected references from the primary literature. The range maps are relatively small, obviously computer generated, but nonetheless useful. Three brief introductory chapters deal with defining what, exactly, is a Neotropical migratory bird and the possible causes of population changes (mostly negative) in various species. There are two large appendices, one on breeding and wintering habitat use (preceded by a succinct description of each habitat) and one on regional statistically significant long (1966–1994) and short-term (1980–1994) population trends (increasing or decreasing), based on data from the FWS Breeding Bird Survey. There is a reasonably thorough literature cited section.

The book is presumably meant as a quick, informative overview, a thumbnail sketch of each species. There is little said about particular behaviors of various species, as there is no paragraph devoted to natural history, as such. Therefore many details are lacking and the reader in search of a reasonably thorough treatment will have to look elsewhere, consulting the references cited, and maybe some that are not cited. For example, in the account of Worm-eating Warbler (*Helmitheros vermivorus*), the winter habitat is described accordingly but there is no mention of this species' interesting and specialized habit of foraging in large, dead leaves, nor is Greenberg's paper documenting this habit cited (Greenberg, R. 1987. Development of dead leaf foraging in a tropical migrant warbler. Ecology 68:130–141). Under Special Habitat Requirements, "Ravines with dense undergrowth" is accurate for Worm-eating Warbler on its breeding range but not its wintering range, and, unfortunately, that distinction is not made. A naive reader could thus be easily misled.

As a second example, in the account of Northern Waterthrush (*Seiurus motacilla*), there is surprisingly no mention of Swartz's historic study of winter site fidelity and territoriality (Swartz, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:169–184), though the account states that the species is "strongly territorial on spring migration at temporary ponds in Texas."

Though this book is lacking in depth, it is nonetheless a useful compendium for anyone whose research interests are focussed on Neotropical migrants.—JOHN C. KRICHER.

ATLAS OF THE BREEDING BIRDS OF MARYLAND AND THE DISTRICT OF COLUMBIA. By Chandler S. Robbins (Senior ed.) and Eirik A. T. Blom (Project Coordinator). University of Pittsburgh Press, Pittsburgh, Pennsylvania. 1996: 479 pp., numerous figures, tables, maps, graphs, and line drawings. $55 (cloth).—This is a state-of-the-art breeding bird atlas that incorporates a wide variety of data bases in addition to the intensive fieldwork data, collected from 1983–1987 by about 800 volunteers. Miniroute data (15 three-minute roadside stops in each atlas block) and Breeding Bird Survey data (BBS; U.S. Fish and Wildlife Service, and Canadian Wildlife Service) provide an index to breeding bird abundance (lack of abundance data is a major flaw in many breeding bird atlases). Other data bases include the Maryland Nest Record File (since 1950), historical records of nesting dating as far back as the mid-1800s, and distribution spot maps compiled during the 1950s. The atlas block was one-sixth of a 7.5-minute U.S.G.S. topographic map, or just

under 10 square miles (25.5 km^2), which is common to many state atlases. However, for the District of Columbia and rapidly changing areas of Maryland, atlasing was conducted at the quarter block level for finer resolution. As a "check" on how satisfactory atlas coverage was, 30 random blocks were intensively atlased by Patuxent Migratory Research staff with the interesting result that their coverage and other coverage produced similar results for common species, but the staff did better at finding rare or secretive species [e.g., Cooper's Hawk (*Accipiter cooperii*) was found in 46% of the random blocks, but only in 14% of the blocks state-wide]. The coverage of blocks state-wide was virtually complete, a feat not accomplished in most atlasing projects.

The introductory section includes a brief but comprehensive review of atlas projects world-wide, and a review of the history of ornithology in the area, including such important figures as Elliott Coues, W. W. Cooke, and A. K. Fisher. A chapter on the environment includes a discussion of soil, physiographic regions, land use (including a detailed historical perspective), human population, and climate. A very brief, but useful chapter deals with the effects of weather on bird populations.

Of 201 species recorded during the atlas period, breeding was confirmed for 194 species, three of which were new for the state. The chapter describing results includes an analysis of short-term bird distribution changes in Howard County, which had been atlased in 1973–1975 as well as 1983–1987.

The species accounts occupy the bulk of the book (399 of 479 pages). Each species account is presented on a pair of facing pages with one page of text and one with maps and graphs. The text includes a wealth of natural history information, including migratory status, habitat preferences, nesting habits, status in the atlas area, and conservation needs. One map shows breeding distribution 1983–1987 ("confirmed," "probable," "possible," and "observed") and a summary table presents the number and percentage of atlas blocks for each status category. Included for most species are a map of breeding distribution in 1958 (previously published), a map of relative abundance with categories representing the percentage of stops the species was recorded on miniroutes, and a BBS graph of population trends. A line drawing of each species accompanies the text. Appendices include lists of plants and non-avian fauna, total atlas species by block, and the literature cited section (23 pages, two columns) alone may be worth the price of the book.

This is an excellent atlas. In addition to the usual useful functions that atlases perform, such as providing data for land-use decisions and research applications, a "snap-shot" in time of breeding bird distribution for future comparisons, this atlas may be of greater-than-usual heuristic value (e.g., for the study of forest fragmentation and for numerical analyses). The book is well edited, sturdy, and attractive. It should be part of every academic library, and of the library of any individual interested in the distribution and conservation of North American birds.—WILLIAM E. DAVIS, JR.

PALEARCTIC BIRDS: A CHECKLIST OF THE BIRDS OF EUROPE, NORTH AFRICA, AND ASIA NORTH OF THE FOOTHILLS OF THE HIMALAYAS. By Mark Beaman. Harrier Publications, Lancashire, UK. 1994: 168 pp. £9.9.—It is manifestly impossible to produce a checklist of English/scientific bird names that will satisfy everyone. Once this is accepted, we can get on with the business of reviewing this admirable effort. British birder and author Mark Beaman has produced an elegant, easy-to-read, and carefully crafted list of English names for all birds known to have occurred in the Palaearctic (which he spells without the second "a") faunal region. There have been a number of such efforts recently for the Western Palaearctic, particularly those sponsored by the BOU Records Committee, *British Birds*, and *Birding World*. Where this one differs, and what makes it so special, is that it is the first to endeavor to give every Palaearctic bird a globally unique English name. It's about time.

Beaman's attractive, soft-covered, slim volume is divided into several parts. The Introduction, especially pp. 6–9, is a splendid apologia for his ideas on vernacular names, and several passages are so utterly charming yet insightful they should be read and reread by

all interested in vernacular names. His sensible, well-articulated viewpoints could well serve as the model for all attempts, whole or in part, to stabilize English names for the world's birds.

Pivotal to this effort yet curiously absent is any discussion of his notion of what constitutes a species, either the traditional Biological Species Concept (BSC), or the more descriptive Phylogenetic Species Concept (PSC), recently so forcefully articulated by C. J. Hazevoet in his *B.O.U. Check-list of the Birds of the Cape Verde Islands* (1995). But close reading of Beaman's extensive Taxonomic Notes makes it clear he relates to the BSC, not the PSC. In the actual Systematic List he gives English and scientific names for most subspecies that have been, or are reasonably likely to be, split or lumped, although he oddly does not discuss the useful format he has adopted.

This brings up an important point. Unlike a number of recent amateur authors, especially those of articles published in some of the newer birding journals, Beaman has actively sought out and integrated technical advice from taxonomists and other ornithologists. The high scientific quality of the finished product clearly reflects both this input as well as the level of technical comprehension Beaman has achieved. At the higher taxonomic levels, he has basically followed the Wetmore/Voous model, eschewing the Sibley and Monroe ordering as experimental and therefore likely to be subject to too many later modifications to be stable enough for his needs. At the generic and specific level he has also used Voous as his base, obviously much modified by recent work. Here he has commendably rejected nearly all of Sibley and Monroe's species splits where he finds that "published supporting evidence is either sparse or lacking, or to [his] mind unconvincing." Nonetheless, most of the names he has chosen do conform to those in Sibley and Monroe.

Three sections occupy the bulk of the book: the Systematic List (pp. 17–62), Taxonomic Notes (pp. 63–99), and Notes on English Names (pp. 100–135). Notes on Distributional Status, Omitted Species, and References conclude the book (pp. 136–168). Beaman takes four pages (10–13) to describe how and why he delimited his "Palaearctic," which is not congruent with that of the 10-volume *Birds of the Western Palaearctic,* or Vaurie's 2-volume *Birds of the Palaearctic Fauna,* or even with Voous. Nonetheless, Beaman's version is not only convincingly presented, it provides a wealth of useful zoogeographic information, especially on the biological significance of elevational bounds.

His literature review is excellent, and covers papers in many languages. Doubtless he will have missed some papers, maybe even critical ones (some have already been pointed out by other reviewers) but the point is that in general, he has done his homework well. I would have liked him to have acknowledged, among other recent name-checklists, *Noms Français des Oiseaux du Monde* (1993), and Bourne and Casement's *RNBWS Checklist of Seabirds* published in *Sea Swallow* (1993), but this is only the first edition of Beaman's book. I fully expect (and hope) it will be revised and updated periodically, when these and other reviewers' criticisms can be addressed.

But what makes Beaman's effort special and nearly unique are the additional premises he has embraced as essential to the creation of a globally-unique checklist of English names. These include trying to conserve English names, especially those in widespread use; recognizing up front that the country where a bird is endemic or where a group is most diverse/abundant should decide what they should be called globally (e.g., longspurs vs buntings)—thus preserving a mix of stints and sandpipers for small calidrines, and hawks and buzzards for buteos; rigorously conserving patronyms, in sharp contrast to Sibley and Monroe who willy-nilly threw out hundreds of ancient English names honoring famous ornithologists the world over; bending over backwards to avoid creating wholly new English names simply because they might better describe some birds than existing names; "in this international era" sedulously replacing all of the diacritical marks such as umlauts and accents that Sibley and Monroe mawkishly removed; to simplify typography, deleting nearly all group-name hyphens (as in hawk-owl, golden-plover, leaf-warbler, etc.); and in literally only a handful of cases where absolutely necessary, resorting to the creation of totally new names.

What results is a felicitous list of the very familiar, the sometimes foreign but still familiar, and the occasionally novel. Clearly, he has tried to reach a workable compromise where European and North American names for the same bird differ, and I think he has succeeded remarkably well. At the very least his choices make interesting reading. For example, loons replace divers, but Black-throated, not Arctic, and Great Northern, not Common; Black-necked, not Eared, Grebe; Great Shearwater; Great, not Eurasian/European, Bittern; Western Reef Egret; Common, not Black, and Velvet, not White-winged, scoters (convincing!); Goosander, not Common Merganser; Rough-legged Buzzard, but Swainson's Hawk; Hen, not Northern, Harrier, Kentish, not Snowy, Plover; Lesser Sand, not Mongolian, Plover; Asian, not Asiatic, Dowitcher; Brünnich's Murre (aha!); American Mourning Dove; Tengmalm's, not Boreal, Owl; Eurasian Skylark, not Sky Lark; Sand Martin, not Bank Swallow; American Cliff Swallow; Common Nightingale, Redstart, Stonechat, and Blackbird; Dark-sided, not Siberian or Sooty, Flycatcher; Grey-streaked, not -spotted, Flycatcher; Eurasian Nuthatch, Treecreeper, and Jay; Common, not Black-billed, Magpie; Western Jackdaw; Common Starling, Chaffinch, and Linnet; European Serin and Greenfinch; Grey-capped, not Oriental, Greenfinch; Arctic, not Hoary, Redpoll; Eurasian Bullfinch; Common, not Red, Crossbill (we'll see how long this lasts); and finally, back to using Reed Buntings.

There are a few places where I find his arguments for choosing one name over another not compelling, his logic faulty, or his applications inconsistent: Little Auk vs Dovekie, where he seems to have forgotten about auklets; Grey Plover and Red Phalarope, and Sora and Brent Goose, where identical arguments lead to opposite conclusions; Pintail Snipe, not Pin-tailed Snipe, but Spoon-billed Sandpiper, not Spoonbill Sandpiper; Long-tailed Duck vs Old-squaw, where his view of linguistic enrichment sustaining Dunnock and Goosander seems to evaporate; and Gyr Falcon, where the implicit argument supporting, for example, Shelduck over Shel[l] Duck, also vanishes.

I really have insurmountable difficulty with only one of his names: the ugly "Pallas's Gull" for Great Black-headed, adopted merely to avoid having to add "Common" to *ridibundus*. Big deal: why can't we have both Black-headed Gull and Great Black-headed Gull? Some rules demand the occasional exception if they are to work. Likewise, I really don't have problems with Crested and Lesser Crested terns; surely we don't need Greater Crested Tern. Taxonomically, he is pretty well up to date, having caught, for example Ahlström's new *Phylloscopus* warblers from southeast Asia, although he curiously missed Steppe Shrike (*meridionalis?*) *pallidiceps*, a likely future split. One odd name choice seems to have been somewhat geopolitically motivated: Red-crowned Crane instead of Japanese or Manchurian (shades of the Persian Gulf vs the Arabian Gulf). Finally, one of his names is particularly mellifluous: "Syrian Serin" just rolls off your tongue.

His taxonomy is a curious mixture of the very conservative (keeping Terek and Common/Spotted sandpipers and the tattlers in their old genera; only partially splitting out all of the Southern Hemisphere skuas; not recognizing Saunders's Tern; not splitting out Black-backed Wagtail) and the liberal (recognizing Fea's and Zino's [sic] petrels as species; splitting Eastern and Western Marsh Harriers; not lumping Canary Islands Oystercatcher; splitting Armenian Gull and Heuglin's Gull) but in most cases reasons are given. The extensive discussions in the Taxonomic Notes (as well as in the Notes on English Names) are very well written: clear, precise, unambiguous, covering both sides of disagreements where appropriate, up to date, and usually compelling. His discussion of the complexities of the genus *Phylloscopus* is an excellent example.

The layout of the book is exceedingly user-friendly, with lots of white space without which this could have been tedious to read. In one of the best proofreading jobs I have ever seen, I have not detected a single error in a type of publication that begs for typos. Even the cover sandgrouse line drawing is exceptionally attractive.

I find this to be one of the best and most useful annotated checklists I have ever seen, setting a standard that future efforts to provide globally unique English names will have to acknowledge. I hope that it will be revised

regularly, and that its author will give serious consideration to applying his considerable skills to a comparable world check-list. We are still waiting for the good one.—P. A. BUCKLEY.

THE BREEDING BIRDS OF QUEBEC: ATLAS OF THE BREEDING BIRDS OF SOUTHERN QUEBEC. Edited by Jean Gauthier and Yves Aubry. L'Association quebecoise des groupes d'ornithologues, the Province of Quebec Society for the Protection of Birds, and the Canadian Wildlife Service, Environment Canada, Quebec Region. 1996 (French edition 1995): 1302 pp., nearly 1500 photographs (more than 300 in color), 300 line drawings, and more than 500 maps. $149.95 (cloth). [Available from: Editions MultiMondes, 930, rue Pouliot, Sainte-Foy (Quebec), Canada G1V 3N9].—This is a massive book—the format is large (28.5 × 33 cm), and it weighs more than 25 kg. Although primarily a breeding bird atlas, it is actually much more. The atlas species accounts do not begin until page 201—the introductory materials occupy the first 87 pages, followed by an extensive section on the bird families of Quebec. The book goes much farther than most atlases in providing in-depth treatment of each species' biology, and provides relative abundance data on birds for each of southern Quebec's ecological regions. An introductory chapter includes three essays that give different perspectives about the history of ornithology in Quebec. This is followed by a chapter on the biogeography of Quebec that includes the major physiographic regions, climate, glaciation, ecoclimate provinces, soils, vegetation, hydrographic system and wetlands, all lavishly illustrated with color maps, satellite and aerial images, maps, and diagrams. A chapter on human impact on the environment is presented in an historical context and also features satellite imagery among the illustrative material. Natural disturbances and habitat conservation are also treated. The section on the bird families of Quebec begins with taxonomy, which largely follows the American Ornithologists' Union Checklist, although DNA-based classifications are discussed. Forty-five accounts of families are supplemented with several hundred color photographs illustrating individual species.

The basic block used in assembling the atlas was a square 10 km per side using the Universal Transverse Mercator grid system. For logistical reasons, the atlasing was restricted to southern Quebec. Total coverage was desired but in remote regions only blocks near access points received coverage, with the northern and western sections receiving less attention. A statistical procedure was employed to estimate relative abundance figures for more than 100 species for 17 ecological (forest type) regions, with relative abundance for a species presented as minimal, low, high, or maximal. The relative abundances, however, cannot be compared among species. More than 900 participants (including about 100 who were hired by local birdwatching clubs) submitted over 200,000 bird records, representing more than 67,000 hours of field work. Breeding was confirmed for 232 species, including five new to Quebec.

The species accounts are typically 2–4 pages (usually 4) with the first text page highlighted by a two-color line drawing of the species, and the facing page having a two-color map showing breeding status ("confirmed" and "possible and probable"). For many species four shades of tan (plus white) indicate levels of relative abundance in the 17 forest regions. A histogram summarizes breeding evidence reported, and a chronology chart shows seasonal occurrence, laying and incubation period, nestling period, and period of dependence of the young out of the nest. The symbols are a bit intimidating, but the key is printed on the inside of the front cover and the facing page which makes for easy access. A small map shows world breeding range, and frequency of occurrence by ecological (forest) region is presented in tabular form. A species profile gives pertinent breeding biology (e.g., clutch size, mating system) and other data (e.g., longevity record, wing span, weight). The text for most species includes an introduction (including field marks for identification) and sections on habitat and behavior, distribution (especially in the atlas region), and history and trends. The habitat and behavior sections are typically extensive, with lots of natural history information, and are generally supplemented with up to a half dozen black-

and-white photographs showing habitat, nest, eggs, adult bird on nest, etc. A section "Notes on territory" is printed below the line drawing of the species.

The species accounts are followed by a series of brief chapters on species diversity and groups of birds with special affinities (e.g., cliff-nesting birds, seabirds of the St. Lawrence). These chapters contain some interesting analyses and are, as usual, profusely illustrated. The appendices have some interesting data, including migratory game bird harvest estimates, a gazetteer, and the scientific and French names for plants and animals mentioned in the text. A glossary makes the book more user friendly. The bibliography is simply staggering—37 pages with five columns per page (over 5000 references).

This is the largest, most lavishly illustrated breeding bird atlas that I have seen. Some might argue that the book might be more usable—it takes two hands and a podium to use this book—if 1000 or so photographs had been deleted (particularly the several hundred color photos of individual species). I have mixed feelings. It certainly is a most impressive book, representing an enormous effort by numerous individuals, but it is expensive and I doubt if many people can afford the price. Certainly it is an excellent contribution to the burgeoning breeding bird atlas literature, and should be part of every academic library. Perhaps the best solution would be to produce an abridged paperback edition which the majority of ornithologists could afford.—WILLIAM E. DAVIS, JR.

BIBLIOGRAPHIE D'ORNITHOLOGIE FRANÇAISE. TOME 2 (1966–1980). By Yves Muller. Service du Patrimoine Naturel and Société d'Etudes Ornithologiques de France, Paris. 1996: 407 pp., 3 numbered text figs., several line drawings, numerous distribution maps, indexes; 290 French Francs (hardcover). [Available from "Universal Book Service, Dr. W. Backuys, P.O. Box 321, 2300 AH Leiden, Holland.]—I love bibliographies. One of my favorites is René Ronsil's "Bibliographie ornithologique française" (1948), which lists all "works published in the French language and in Latin in France and the French colonies from 1473 to 1944." I was thus delighted when I received for review volume two of Yves Muller's "Bibliographie d'ornithologie française," a work that, once complete, will cover the period from 1945, when Ronsil's undertaking stopped, to 1990. I also love libraries. During my career I have been lucky to be associated with two institutions that have arguably the best ornithological and natural history libraries in the western hemisphere, Harvard University's Museum of Comparative Zoology and the American Museum of Natural History. For others who are not so fortunate, however, and must be content with libraries having incomplete holdings, good bibliographic works are the tools of necessity.

Outstanding ornithological bibliographies besides Ronsil's are John T. Zimmer's "Catalogue of the Edward E. Ayer Ornithological Library" (Field Museum of Natural History 1926), the bibliographies in the "Ornithological Gazetters of the Neotropics" by Raymond A. Paynter, Jr. and his collaborators (published by the Museum of Comparative Zoology at Harvard University from 1975 to 1995), and Clifford B. Frith's annotated bibliography of the Papuan Subregion, 1915–1976 (Bulletin of the American Museum of Natural History, 1979).

Yves Muller's "Bibliographie d'ornithologie française, tome 2 (1966–1980)," is the second of a three-volume work. Volume 1, dealing with the period 1945–1965, appeared in 1992 and volume 3, which will include the years 1981–1990, is in preparation. After completion Muller's work will cover 45 years, from the difficult post World-War II period to the tremendous recent development of French ornithology, thus complementing and bringing up to date Ronsil's bibliography. However, although Muller's bibliography is a successor to Ronsil's, it differs from it in two significant respects. First, whereas Ronsil's bibliography included works only in the French and Latin languages (whether these works had been published in France or outside that country), Muller's includes also "publications in foreign languages." Second, whereas Ronsil's bibliography not only included works on the birds of France or her colonies, but also works in French or Latin dealing with the birds of other countries, Muller's only includes works

concerned with the birds of "Metropolitan France" (p. 10; what the French call "l'hexagone"). Thus the island of Corsica is included but "the Anglo-Norman islands of Jersey and Guernesey [sic]" and the French colonies or former colonies are excluded. In Muller's words "[My] work thus differs fundamentally from that of Ronsil" (p. 10). In a way this is a pity, because users of Ronsil's and of Muller's works will have to remember these differences, which make comparisons between these two massive bibliographic efforts difficult. Although I respect Muller's decisions (after all, one has to set limits to any work), I am sorry that he did not include publications (whether in French or other languages) about the birds of French colonies, ex-colonies, or territories such as New Caledonia, Tahiti, or Réunion, which would have made his bibliography more comparable to Ronsil's and also useful to a wider audience. Muller is aware of these problems as he wrote that "A revision of Ronsil's bibliography is contemplated, both at the level of the list of references and that of an index, presently quite inadequate" (p. 10). Three more items must be mentioned before analyzing the book further. Within the linguistic and geographic limits cited above, Muller has included works about "birds studied in their natural environment" but not general ornithological works about anatomy, physiology, and systematics, or works about captive held birds. As a systematist I regret the exclusion of systematics. Next, Muller has included "scientific" rather than "popular" works. Finally, he has included only publications that are available in libraries and thus are accessible to the public. Muller's criterion of what constitutes a publication excludes documents such as privately circulated reports and some university theses (like masters' theses) that are not "systematically deposited in libraries" but includes PhD-type theses which are found in libraries and are thus "available to every researcher."

How good a tool is Muller's "Bibliographie d'ornithologie française"? I believe that it is excellent. There are probably missing references in Muller's book but I haven't found them. Muller has searched for relevant publications in many journals, not just obvious ones like *Alauda, Gerfaut, L'Oiseau et la Revue Française d'Ornithologie, Nos Oiseaux,* or *Journal für Ornithologie,* but also local ones like *Bulletin de l'Association philomatique d'Alsace-Lorraine, Riviera scientifique,* or *Mémoires de la Société Académique de l'Aube.* He has also searched for references in the bibliographies published in *L'Oiseau* since 1969 and in the bibliographic lists included in all the articles he consulted. Muller expressed his debt to the librarians and to the libraries of the Zoological Museum in Strasbourg, of the Société Ornithologique de France in Paris, and of the Swiss Ornithological Institute in Sempach. (As I am reviewing a bibliographic work on the birds of a European country, it is appropriate to say that the Swiss Ornithological Institute has probably the best ornithological library in Europe, thanks to Raymond Lévêque's phenomenal knowledge of the avian literature and his tireless efforts to acquire just about every ornithological publication that he could obtain.)

Muller's exhaustive search for bibliographic entries has led him to include 4250 references, 246 as complements to the first volume and 4004 for the period 1966–1980. Muller documents the phenomenal increase in the number of ornithological publications on the birds of France since 1945: from a yearly average of 54 in the period 1945–1949 to a maximum of 442 for the year 1980 alone. Muller highlights several aspects of this growth. He calls 1945–1965 "the period of ornithological exploration in France," qualifies the 1970s as the decade when field ornithology truly took off in France, and emphasizes the importance of university research in ornithology in the period 1966–1980. Whereas only two PhD-type theses on the French avifauna were produced in the period 1945–1965, no fewer than 57 came out in 1966–1980. Similarly, whereas only two ornithological journals, *Alauda* and *L'Oiseau,* were published at the beginning of the 1945–1965 period, many were started after 1953. To quote Muller (p. 17): "Ninety-seven periodicals published observations on the birds of France during the years 1945 to 1965. In the next 15 years, this number climbed to 212, essentially as a result of several dozen new ornithological journals." The nine journals with more than 100 publications each in 1966–1980 are *Alauda, le Héron, Nos Oiseaux, L'Oiseau et la Revue Française d'Ornithologie, le Jean-le-Blanc, le Lien or-*

nithologique d'Alsace, le Grand-Duc, le Passer, and *Penn ar Bed.* How many of these periodicals do you consult? (Incidentally, *L'Oiseau* no longer exists. After a "merger," the only ornithological journal now published by the Société d'Etudes Ornithologiques de France is *Alauda.*)

The "Bibliographie d'ornithologie française" for 1966–1980 includes two maps showing the geographical distribution of ornithological work in France (pp. 18–19), complements to the period 1945–1965 (pp. 23–30; references are number-coded from 02402 to 02647), the references for 1966–1980 (pp. 31–172; number-coded from 02468 to 06660), the list of periodicals (pp. 174–177), the index of periodicals (pp. 177–196, listing the number-coded references for each periodical), a geographic index by administrative region and departments (pp. 198–220), a taxonomic index (pp. 222–351; giving the French and Latin names of species following the sequence of K. H. Voous in *Ibis* 1973 and 1977), a thematic index (pp. 354–362; 54 topics ranging from "alimentation" to "vol" and including subjects like "cannibalisme," "invasions," "pollution," "prédation," "protection," and "territorialité"), and a series of attractive maps (pp. 366–400; which are not an atlas of the French avifauna but illustrate the geographic distribution of references for 422 species). The book ends with three indexes (pp. 402–407): geographic, vernacular French names, and scientific (Latin) names.

In his preface to the "Bibliographie" the genial president of the Société d'Etudes Ornithologiques de France Camille Ferry wrote: "I learned in grade school that good workers have good tools. Given the tool Yves Muller has given us, if there remain bad workers in ornithology it will certainly be their own fault." Indeed. With Ronsil's earlier book and volumes 1 and 2 of Muller's bibliography ornithologists have an unsurpassed set of tools to guide them in their bibliographic research on the avifauna of France. In Muller's debt are French ornithologists, of course, and also all of us who are interested in Palearctic birds or who try to keep up with the flood of literature. At a broader level Muller's book will be indispensable to those who protect birds and their habitats in France and elsewhere in western Europe. I hope that Muller will consider including, in volume 3 or in a fourth volume, bibliographic entries pertaining to the birds of former French colonies and of French overseas territories. While waiting for volume 3, I congratulate Yves Muller for a job well done and pay homage to the sponsors of his book, the Service du Patrimoine Naturel, the Institut d'Ecologie et de Gestion de la Biodiversité, the Muséum National d'Histoire Naturelle, the Société d'Etudes Ornithologiques de France, the Ministère de l'Environnement, the Office National des Forêts, and the Office National de la Chasse.—FRANÇOIS VUILLEUMIER.

THE BIRDS OF TOGO. By Robert A. Cheke and J. Frank Walsh. British Ornithologists' Union Check-list No. 14. 1996; ca 230 pp., hardback, 9 figs., gazetteer, 39 color photos of habitat and 14 of birds. £22.00 (UK), £24.00 (overseas) incl. postage. [Available from British Ornithologists' Union, c/o The Natural History Museum, Tring, Herts. HP23 6AP, UK.]—Togo is a little-known west African republic hardly bigger than New Hampshire and Vermont (combined), strategically located biogeographically. Along with equally obscure Benin, Togo occupies the narrow "Dahomey Gap" between Ghana and Nigeria, where a tongue of African Savanna reaches nearly to the Gulf of Guinea, effectively interrupting the continuity of lowland Guinea forest. Given apparent speciation events in birds and other life forms on either side of the Gap, better knowledge of life within the Gap seems requisite to understanding the evolutionary forces at work. The authors, both associated for a number of years with the World Health Organization in Togo, have combined their observations (and others') with a scholarly compilation of the avian literature and specimen record. The latter task was particularly difficult as a result of the complex colonial history of the region, especially use of the name "Togo." The result is the first comprehensive, credible baseline avifauna for any portion of the Gap, accrediting 624 spp. to the Republic. The annotated list is supplemented with much other useful information such as an outline of Togo's environment, color habitat photos, and banding recoveries (all of birds banded north of the Sahara) that one has come to expect of the fine BOU Check-list series. I recommend this well-done book to all

students and libraries with an interest in the region's birdlife and zoogeography.—P. WILLIAM SMITH.

AN ANNOTATED CHECKLIST OF THE BIRDS OF THE ORIENTAL REGION. By Tim Inskipp, Nigel Lindsey, and William Duckworth. Oriental Bird Club, The Lodge, Sandy, Bedfordshire, U.K. 1996: 294 pp., including a map delineating the Indomalayan region. £9.95 (paper).—Certainly no young ornithological club ever integrated a progressive and open professionalism with the best sort of amateurism as has the Oriental Bird Club. This club is perhaps best known for its annual scientific bird journal, the *Forktail,* which, like the checklist under review, is beautifully and professionally produced. The most remarkable thing about all of this is that these products are almost exclusively produced by bird-lovers in their spare time, not for pay. They have set a high standard indeed.

This annotated checklist is testament to how far this organization has come in little more than a decade. For here is a handsome, inexpensive, data-rich but compact nomenclatural and taxonomic compilation of the avifauna of some 2500 species that inhabits the region from Pakistan north to the Himalayas, eastward to southern China, Taiwan, the Philippines, the Greater and Lesser Sundas, and Wallacea. I suspect this is but the first of an array of excellent publications that the Club will issue on the birdlife of this biotically and culturally complex segment of the earth.

The work begins with an explanation of its aims, the geographic coverage, methods of taxonomic treatment, a discussion of species concepts, and construction of the English names. These are fundamental to understanding how the list was put together, and the authors should be praised for their transparency. Perhaps best of all is that most or all of the usages and treatments in the list are based on published taxonomic and systematic opinion—the reader can thus trace back to the source of anything that seems problematic—a most useful ability for an avifauna as little-studied and problematic as this one.

The introductory discussions are comprehensive, well-argued, and well-annotated. The authors accept the use of the biological species concept, although they fairly review the various arguments in favor of the competing phylogenetic species concept. For higher level organization, the list generally follows the treatment of Sibley and Monroe, and again here the authors provide useful clarifying discussion of why they chose this over other, more traditional, options. Their rules for English nomenclature are explained in detail. A series of codes for important references, conservation and distributional status, and species-limits is presented in tabular form in the introduction and used extensively in the checklist. These codes perhaps constitute the greatest challenge to the reader—there are too many to quickly memorize, and the coding is not explicit enough for mnemonic purposes.

Now to the checklist. It is nicely laid-out in a double-column format, the accepted English and scientific names to the left, and the explanatory material to the right. This latter includes recent synonyms, other treatments, and comments on species limits. Because of the huge number of poorly-studied forms, this annotation is critical to the utility of the checklist, and the authors greatly increased the reference value of the work by compiling these data for the benefit of the reader. The best thing about the treatment is its transparency—wherever practical, competing views are noted, so that the reader gains access to the diversity of opinion in a ready fashion in this single list. One can quickly pin-point the troublesome groups—they are the ones with the profuse annotation.

Perhaps some will be disappointed that there is no distributional data included in the list. That was clearly beyond the scope of this project, whose goal was to construct a practical baseline nomenclature for use by ornithologists, conservationists, natural resource managers, and birders in the Indomalayan region. This they have done with great skill. One suspects that a next permutation will be a distributional checklist—which perhaps will require more than one volume. The checklist is not perfect, and naturally the authors made some decisions I disagree with—but that's to be expected in such a large analysis.

The bibliography includes 814 references. There are well-designed comprehensive indexes of English and scientific names. This is a must-buy for any ornithologist with an interest in South and Southeast Asia or for those interested in the systematics and nomenclature of birds of the world. The quality is superb, and price is right.—BRUCE M. BEEHLER.

The Wilson Bulletin
Instructions to Authors

Be advised that manuscripts that do not conform to these guidelines will not be accepted for publication.

I. General Instructions

Prepare manuscripts on 8.5 × 11 inch paper (if your standard-sized paper is A4 [210 × 297 mm], please leave at least a 40-mm margin at bottom so that manuscript can be copied on 8.5 × 11 inch paper without lines being cut off at the bottom). Double-space throughout, including tables, figure legends, and literature cited. Leave at least a 1-inch (25-mm) margin on all sides. Do not hyphenate words at ends of lines. Please be sure and submit **four copies** of the manuscript to: Robert C. Beason, Editor, Biology Dept., State Univ. of New York, 1 College Circle, Geneseo, NY 14454-1401.

If possible, use italic type instead of underlining words to be italicized. Only the following Latin terms should be italicized: *in vivo, in vitro, in utero, in situ, ad libitum, a priori, a posteriori.* All other Latin terms (except scientific names) should be left unitalicized.

Cite each figure and table in the text. Tables and figures must be sequenced in the order cited. Use "Figure" only outside of parentheses; otherwise, use "Fig." if singular, "Figs." if plural (e.g., Fig. 2; Figs. 2 and 3; Figs. 3-6). To cite figures from another work, write figure or fig. in lowercase (e.g., figure 2 in Smith (1980); Smith 1980: fig. 2; Jones 1987: table 5).

All measurements are to be given in SI units. Use continental dating (e.g., 29 September 1992), the 24-hour clock (e.g., 08:00 and 23:00), and standard time (not daylight savings time). Specify that it is Standard Time (e.g., EST for Eastern Standard Time) at first reference to time of day.

English proper names of bird species that occur in North and Middle America should follow the 6th edition of AOU's Check-list of North American Birds and its supplements. Names for other species of birds should follow an appropriate standard. English proper names of birds should be capitalized, but not the English names of other organisms.

Use the following abbreviations: s (second), min (minute), h (hour); designate temperature as °C. Do not abbreviate day, week, month, or year. User-defined abbreviations should be written out in full words the first time the term used in text. Abbreviate thereafter: "Second-year (SY) birds . . . We found SY birds in large numbers."

Use the following statistical abbreviations: ANOVA, SD, SE, df, CV, ns, *n, P, r, F, G, t*-test, *U*-test. Other statistical abbreviations, in general, conform to sixth edition of Scientific Style and Format: The CBE Manual for Authors, Editors, and Publishers (1994, Cambridge Univ. Press, Cambridge, UK).

Write out numbers one to nine unless a measurement, but use numerals for larger numbers (e.g., three birds, 6 mm, 12 days, 2 min). If number is in a series with at least one number being 10 or more, then use all numerals (e.g. 6 males and 13 females). Use 1,000 not 1000, 0.01 not .01, and 50% instead of 50 percent.

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Dissertations, books, chapters:

American Ornithologists' Union. 1983. Check-list of North American birds, 6th ed. American Ornithologists' Union, Washington, D.C.

Freeman, S. 1991. Molecular systematics and morphological evolution in the blackbirds. Ph.D. diss., Univ. of Washington, Seattle.

Gaunt, A. S. 1988. Interaction of syringeal structure and airflow in avian phonation. Pp. 915-924 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Sciences, Ottawa.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London, UK.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* The birds of North America, no. 47 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Kear, J. 1970. The adaptive radiation of parental care in waterfowl. Pp. 357-392 *in* Social behavior in birds and mammals (J. H. Crook, Ed.). Academic Press, London, UK.

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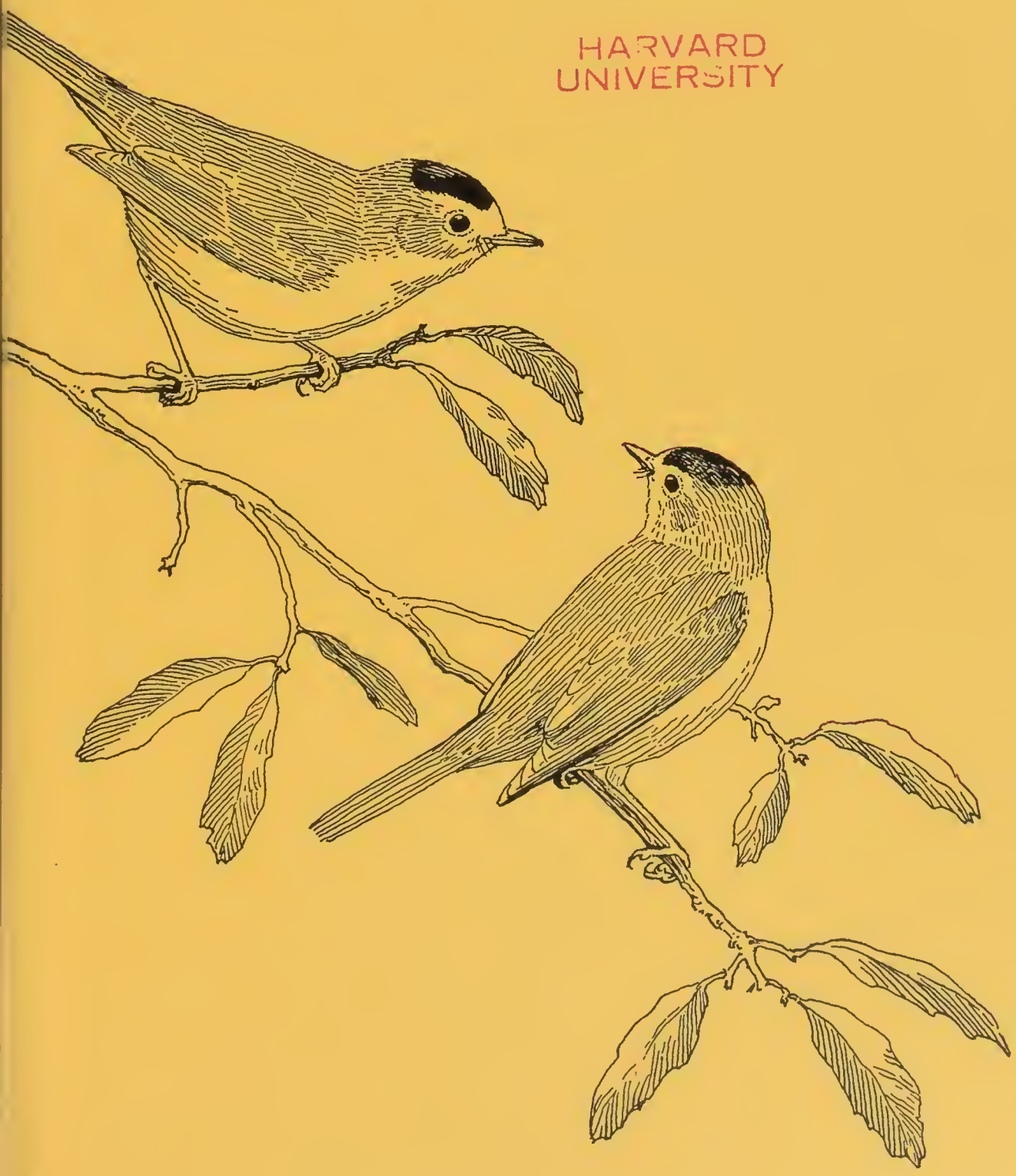

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FRONTISPIECE. "Masked" boobies from the eastern Pacific Ocean. Above, Masked Booby (*Sula dactylatra*); below, Nazca Booby (*Sula granti*). Both photos taken on Clipperton Island, May 1987 by R. L. Pitman.

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GEOGRAPHIC VARIATION AND REASSESSMENT OF SPECIES LIMITS IN THE "MASKED" BOOBIES OF THE EASTERN PACIFIC OCEAN

ROBERT L. PITMAN[1] AND JOSEPH R. JEHL, JR.[2,3]

ABSTRACT.—Two distinct forms of Masked Booby (*Sula dactylatra*) occur in the eastern Pacific: (1) a yellow-billed form that includes a population on Clipperton Island and islands off western Mexico (*S. d.* "*californica*"), and another, unnamed, population on Las Islas Desventuradas, Chile, and (2) an orange-billed form [*S.* (*d.*) *granti*] that nests almost exclusively on the islands of the Galápagos and on Malpelo Island, Colombia. Quantitative comparisons, including discriminant function analysis (DFA) of standard morphological characters indicated that yellow-billed populations are only marginally different from one another, and neither is consistently separable from *S. d. personata*, a yellow-billed form that ranges over most of the tropical Pacific. Further, we found no consistent differences in bare-part coloration or plumage among yellow-billed populations. In contrast, DFA indicated morphological differences between orange- and yellow-billed populations. The orange-billed bird is smaller with a significantly shorter, shallower bill, shorter tarsus, and longer wings and tail. It is also more sexually dimorphic and has distinct plumage characters. Biological observations also support the distinctness of orange-billed birds. They typically nest on cliffs and steep slopes, whereas yellow-billed forms nest mainly on low, flat areas. A difference in habitat preference at sea resulted in a parapatric distribution: orange-billed birds away from colonies concentrated in nearshore waters off the coast of the Americas, whereas the yellow-billed forms foraged much farther offshore. Most importantly, orange- and yellow-billed birds paired assortatively where they nested sympatrically. Thus, based on morphological and biological differences, including positive assortative mating, we recommend that *Sula granti* be recognized as a separate species, the Nazca Booby.
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Geographic variation in the Masked (or Blue-faced) Booby (*Sula dactylatra*) has been over-described but under-studied. Most of the seven proposed races of this common pantropical seabird date from an era of excessive splitting and were based almost entirely on foot and bill coloration. Plumage and size (with one exception) were ignored, perhaps because few collections contained enough material to allow study of variation in those characters. Although coloration of bare parts (bill, face, legs, feet, and eyes) has been important in sulid systematics (Nelson 1978), conducting comparative studies of these features using only dried museum specimens or notations on specimen labels is almost impossible. Given those complications, and the continued lack of large series of specimens, it is not surprising that no thorough study of geographic variation in this species has ever been attempted. Analysis was further impeded by the residual authority of R. C. Murphy (1936), who was reluctant to accord much weight to color characters in boobies because of their sexual dichromatism as well as individual variation. Murphy's caution was understandable, but it led him to overlook characters that we con-

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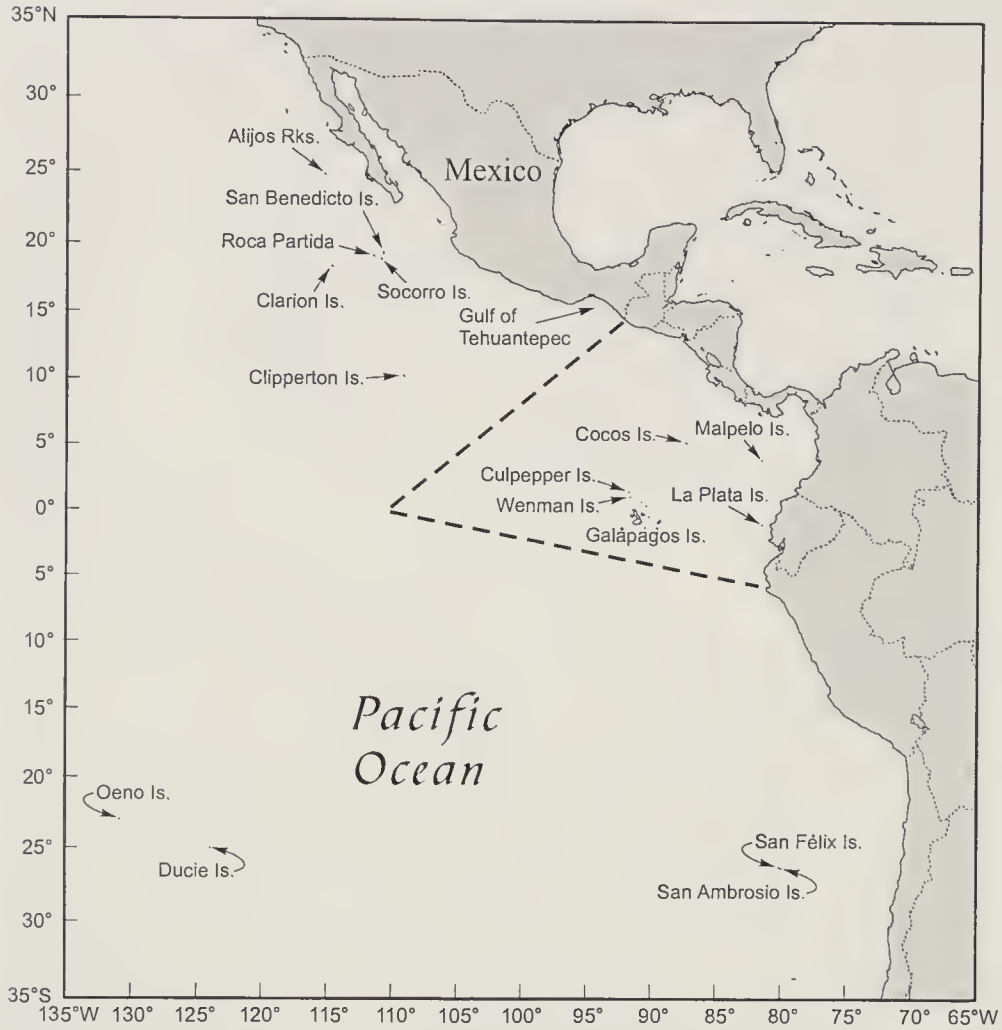

FIG. 1. The eastern Pacific Ocean showing location of "Masked" booby colonies and other sites mentioned in the text. Dashed line separates the major yellow-billed (*Sula dactylatra*) colonies to the north and south from the central orange-billed (*S. granti*) colonies.

sider meaningful, especially because bare-part coloration in Pelecaniformes is clearly important in social signaling and probably in individual recognition as evidenced by interspecific, and often intraspecific, color variation in, for example, cormorant facial skin and iris coloration, tropicbird bills, frigatebird eyerings, pelican and frigatebird pouch coloration, and booby foot, bill and face coloration (Van Tets 1965, Nelson 1978).

This review of geographic variation, which is restricted to Masked Booby populations in the eastern Pacific, was prompted by two sets of field observations. The first was the recognition that there are three clear assemblages that can be defined on the basis of bill color (yellow-billed = YB; orange-billed = OB), and breeding locale: (1) a northern YB population (sometimes recognized as *S. d. californica*) nesting from Clipperton Island to Alijos Rocks; (2) a central OB population [*S.* (*d.*) *granti*], nesting mainly on the islands of Galápagos and Malpelo, with much smaller numbers breeding from Isla La Plata, Ecuador, to San Benedicto Island, Mexico, and (3) an unnamed YB population (often incorrectly identified as OB; Murphy 1936, Johnson 1965, Bahamonde 1974, Nelson 1978) on the Islas Desventuradas (San Félix and San Ambrosio), Chile (Frontispiece, Fig. 1). The second and more stimulating observation was that OB and YB birds differ in pelagic distribution and nesting habitat preferences, and, evidently, pair assortatively where they occur sympatrically. In this paper we review the morphological and biological characteristics of these Eastern Pacific populations and argue that *S. granti* is specifically distinct from YB forms.

METHODS

We base this review on: (1) examination of museum specimens (see acknowledgments) of birds taken in the immediate proximity of nesting colonies, or whose

provenance can be determined from characteristics described below; (2) the systematic literature; (3) our field work in the eastern Pacific, which includes visits to all of the known Masked Booby colonies; and (4) an extensive series of photographs of boobies at sea and in the colonies.

We compared morphological characters of specimens from three separate YB populations in the eastern Pacific with OB specimens. These populations were (1) *S. d. californica* (YB), which we will refer to as "Mexican" birds, (2) an unnamed YB population on colonies off Chile, which we will refer to as "Chile" birds, (3) *S. d. personata* (YB), and (4) *S. (d.) granti* (OB). For *S. d. personata,* we used specimens from the nearest adjacent colonies in the central Pacific, Ducie (25° S, 124° W) and Oeno (23° S, 131° W); both are about 4000 km equidistant from Clipperton, the Galápagos, and the Chilean islands. We used the standard morphological characters of bill length, bill depth, bill ratio (depth/length), wing and tail length (Table 1). Boobies are difficult to measure and dimensions obtained by different researchers may not be fully comparable. For example, data in Marchant and Higgins (1990) indicate that museum specimens of *S. d. fullagari* are smaller than living birds, as expected because of shrinkage of skins, but that living *S. d. personata* from Raine Island, Australia, are smaller than skins. For consistency, all original measurements in this report were made by JRJ.

We tested for significant differences in each morphological variable using ANOVA and made multiple comparisons with a Tukey test. We use a discriminant function analysis (DFA) on log-transformed data to determine the effectiveness of five morphological variables (bill ratio excluded) in separating YB and OB forms. In all quantitative comparisons, we treated males and females separately to eliminate variation imposed by sexual dimorphism. We give results of the DFA for males only, because patterns for females were similar. All analyses were performed using SYSTAT (Wilkinson 1989) on an IBM-compatible computer.

We visited all of the known Masked Booby colonies in the eastern Pacific, noting colony size and bill color of roosting and nesting birds (Table 2, Fig. 1). We collected data on at-sea distributions from nine research cruises between 1983 and 1990 (prior to that no distinction was made between YB and OB birds). Details of at-sea methods are outlined in Pitman (1986). Note that cruises on which the forms were distinguished are seasonally biased in that 94% of the survey days (n = 266) on which sightings were made were in the second half of the year.

RESULTS

A brief taxonomic review.—Geographic variation in Masked Boobies, as understood early in this century, was summarized by Mathews and Iredale (1931:75): "Rothschild in 1915 proposed five subspecies as follows: *S. d. dactylatra* (Lesson [1831]) from Ascension Island and South Atlantic coasts with bill horny blue-gray, very slender, feet and legs yellow; *S. d. melanops* Hartlaub [1859], from Western Indian Ocean, with bill greenish-yellow, slender, feet and legs slaty-blue to dull black; *S. d. personata* (Gould [1846]) from Western Pacific with bill yellow, very stout and large, feet and legs greenish-blue; *S. d. californica* Rothschild [1915], from Coasts of California and Central America, with bill bright yellow, very thick, feet and legs orange; and *S. d. granti* Rothschild [1902], with bill red and feet bluish-green from Galápagos Islands." An additional form, *S. d. bedouti* from Bedout Island, off western Australia, was ignored by Rothschild; it was said to differ from *S. d. personata* "in its much smaller size, especially in the bill; and in having blue feet" (Mathews 1913:189). Recently, O'Brien and Davies (1990) described *S. d. fullagari* from Lord Howe, Norfolk, and the Kermadec islands, which was characterized as having a dark eye. These characters, as well as those of the Chile birds, are summarized in Table 3.

Early in this century there was confusion about the identity of *S. (d.) granti* from the Galápagos, because it was originally identified as a Peruvian Booby, *S. variegata* (e.g., Rothschild and Hartert 1899, Snodgrass and Heller 1902, Beck 1907, Gifford 1913). Rothschild (1902) corrected the mistake and designated the originally misidentified specimen as the type of a new species, *Sula granti.* According to Sharpe and Ogilvie-Grant (1898: 435) the bill in the dry skin was "red, paler toward the tips of the mandibles" and the legs were "yellowish brown." [Note that these characters differ somewhat from those reported by Mathews and Iredale (1931, above)]. The label of the type specimen (AMNH 729,228) contains no information on coloration.) Snodgrass and Heller (1902:512) wrote that Galápagos boobies were "identical in plumage" to those from Clipperton and the Revillagigedos but differed in bill color; they also alleged "some differences in proportions." Gifford (1913:92–93) expanded on this, reporting that Galápagos birds had "a decidedly longer wing, and . . . a relatively shorter tarsus . . . than has the average *Sula cyanops* [=*S. dactylatra*]." Even so, Rothschild (1915:44)—without acknowledging his peers or presenting any morphometric infor-

TABLE 1. Dimensions of "Masked" boobies (*Sula granti* and *S. dactylatra*) (measurements in mm). Locality of specimens and references are listed below each population.

	Male				Female			
	n	$\bar{x}$	Range	SD	*n*	$\bar{x}$	Range	SD
S. granti[a]								
Galápagos; Malpelo; at sea off Ecuador, Guatemala, Peru, Gulf of Panama (this study)								
Bill length	19	101.9	96.3–107.2	3.12	16	105.0	100.0–113.2 100.0[b]	3.79
Bill depth	20	33.3	30.4–35.8	1.88	15	35.4	33.5–38.0 34.5[b]	1.56
Bill ratio[c]	19	0.32	0.29–0.36	0.017	15	0.34	0.32–0.34 0.34[b]	0.018
Wing	20	437.8	410–467	17.02	16	460.8	438–483 438[b]	16.06
Tail	20	175.4	165–185	6.09	16	179.9	160–194 176[b]	8.76
Tarsus	20	54.1	50–60.4	3.02	16	57.43	52.3–63.0 55.9[b]	2.61
S. d. californica[a]								
Alijos Rocks, Revillagigedos, Clipperton (this study)								
Bill length	12	103.0	99.5–106.5	2.61	9	102.1	98.8–109.2 100.5[b]	2.96
Bill depth	12	36.3	33.5–40.5	1.69	9	37.2	35.2–39.8 38.5[b]	1.66
Bill ratio[c]	12	0.35	0.33–0.38	0.016	9	0.36	0.35–0.40 0.38[b]	0.018
Wing	12	434.3	405–462	19.70	9	433.2	405–450 450[b]	16.38
Tail	12	174.8	160–197	13.62	9	175.6	163–196 196[b]	10.91
Tarsus	12	56.4	53.5–60.3	2.35	9	57.9	53.0–61.8 55.9[b]	2.93
S. d. "Chile"[a]								
Chile: San Félix, San Ambrosio (this study)								
Bill length	4	105.1	102.1–107.5	2.28	8	106.2	101.9–110.0	3.16
Bill depth	4	36.2	33.8–38.5	2.19	8	37.1	35.5–38.2	1.05
Bill ratio[c]	4	0.35	0.33–0.38	0.021	8	0.35	0.34–0.35	0.008
Wing	4	445.6	434–462	10.97	8	466.1	455–481	8.98
Tail	4	183.2	178–192	5.76	8	187.2	165–196	10.08
Tarsus	4	60.7	57.5–64.7	2.85	8	62.4	58.5–65.8	2.81
S. d. personata[a]								
Ducie, Oeno (this study)								
Bill length	4	104.4	95.5–109.5	6.38	8	105.8	102.8–110.8	2.68
Bill depth	4	36.8	34.5–38.5	1.7	8	38.2	35.7–42.8	2.25
Bill ratio[c]	4	0.35	0.34–0.37	0.015	8	0.36	0.34–0.39	0.018
Wing	4	436.5	430–445	6.56	8	453.5	442–460	6.78
Tail	4	180.2	157–195	16.40	8	185.5	176–196	6.37
Tarsus	4	58.2	52.5–60.7	3.82	8	60.0	56.8–63.2	2.02
S. d. bedouti								
Bedout Is., Australia (O'Brien and Davies 1990)								
Bill length	3	104.3	103–106	1.2	3	103.9	101.0–105.8	2.1
Wing	3	413	401–420	8	3	425	422–430	3
Tail	3	171	165–175	3	3	177	172–186	6
Tarsus	3	53.9	51.0–51.7	2.8	3	54.4	52.0–58.4	2.8

TABLE 1. Continued

	Male				Female			
	n	$\bar{x}$	Range	SD	*n*	$\bar{x}$	Range	SD
S. d. fullagari								
Lord Howe Is. (O'Brien and Davies 1990)								
Bill length	14	108.3	104–114	3.3	7	109.9	105.0–115.4	3.1
Wing	14	442	429–455	6	7	452	430–468	12
Tail	11	187	175.0–202.7	11	12	190	174–205	12
Tarsus	14	58.9	53–65	3.3	7	61.0	54–65	3.51
S. d. dactylatra								
Ascension, Fernando de Noronha (Murphy 1936)								
Bill length	9	95.6	92.6–97.2		7	95.7	91.6–99.0	
Wing	9	424	406–433		7	429	417–440	
Tail	9	166	153.0–173.2		7	164.6	151.3–180.0	
Tarsus	9	54	53.0–56.2		7	53.4	52.0–54.6	
S. d. melanops								
Red Sea, Indian Ocean (Brown et al. 1982)								
Bill length	6	100.7	97–104					
Wing	6	421	407–430					
Tail	6	176	169–180					
Tarsus	6	56	51–58					

[a] Measured by J.R.J.
[b] Dimensions of type specimen.
[c] Bill depth/bill length.

mation to the contrary—reversed his earlier stand and decreed there was "absolutely no other difference" between *S. granti* and *S. d. californica* except bare-part coloration. He reduced *S. granti* to subspecies rank, a position subsequently adopted by Murphy (1936) and Nelson (1978).

Yellow-billed populations in the eastern Pacific.—The yellow-billed Masked Booby that breeds north of the equator in the eastern Pacific, sometimes recognized as *S. d. californica* (e.g., AOU 1957), nests from Alijos Rocks, Mexico, south to Clipperton Island. [A single YB individual nesting among a colony of OB boobies on La Plata Island in September 1989 (Table 2) was of unknown provenance]. The total population is on the order of 65,000 individuals, 95% of which occur on Clipperton (Table 2).

Rothschild (1915:43–44) described *S. d. californica* from an adult female taken at San Benedicto Island (measurements of type specimen in Table 1). Asserted characters were "bill bright yellow, very thick; feet and legs orange." Rothschild's leg color description is inconsistent with our observations: YB Masked Boobies that currently nest on Clipperton and San Benedicto have legs that are either blue or greenish blue, or greenish yellow (Table 3). Rothschild also wrote that *S. d. californica* had a "much larger and stouter bill" than *S. d. dactylatra.* He made no comparisons with *S. d. melanops* or *S. d. personata,* although he characterized the latter as "bill yellow, very stout and large; feet and legs greenish blue."

South of the equator, James P. Chapin in 1935 discovered Masked Boobies nesting on Las Islas Desventuradas (San Ambrosio and San Félix), Chile (Murphy 1936). The colony is small, comprising several hundred (Bahamonde 1974) to perhaps a few thousand pairs, all yellow-billed (Jehl 1973, unpubl. data). Bare-part coloration in this population as described by Bahamonde (1974) is evidently paraphrased from Murphy's (1936) description of *S. d. granti* (in which Murphy mistakenly included the Chilean population) and cannot be credited as independent or authoritative.

Our quantitative and qualitative comparisons support the view that the YB populations

TABLE 2. Location, dates of visits, and size of breeding colonies and roosting sites of "Masked" boobies in the eastern Pacific Ocean. Listed are number of individual birds (+ = present). Dashed horizontal lines separate primarily orange-billed (OB = *Sula granti*) colonies from yellow-billed (YB = *S. dactylatra*) colonies to the north and south (see Fig. 1).

Site	Number of YB individuals (% of population)	Number of OB individuals (% of population)	Comments	Source
Alijos Rocks	+	+	Oct 1983; 100 breeding, mostly YB; a few OB roost, some may breed	Pitman 1985, R. L. Pitman, unpubl. data
Clarión	757–937 (>99)	min 3 (<1)	Feb 1988	Howell and Webb 1989, 1990
San Benedicto	1,166–1,196 (>99)	4 (<1)	Feb 1988	Howell and Webb 1990
	2,450 (98)	50 (2)	Nov 1990	R. L. Pitman, unpubl. data
Roca Partida	+	+	Aug 1987, Feb 1988, Aug 1989; both forms roost, neither confirmed breeder; max. roosting numbers 5 Aug 1989: 48 YB, 5 OB	Howell and Webb 1990, R. L. Pitman, unpubl. data
Socorro Island	+?	+?	Not breeding; up to 10 individuals roosting; bill color not recorded	Wehtje et al. 1993, R. L. Pitman, unpubl. data; J. Jehl, unpubl. data
Clipperton Island	61,339 (99.8)	150 (0.2)	4 visits, 1986–1990	Pitman et al., unpubl. data
Cocos Island	0	0	Oct 1989; 3 YB roosting; no breeding	Slud 1967, R. L. Pitman, unpubl. data
Malpelo Island	0	24,034 (100)		Pitman et al. 1995
Galápagos	0	50,000–100,000 (100)	YB individuals occasionally occur on northern islands (Wenman and Culpepper); breeding status unknown	Nelson 1978, D. J. Anderson, pers. comm.; R. L. Pitman, unpubl. data
La Plata	1 (<5)	794 (>95)	Both forms breed; minimum I YB Sept 1989	Ortiz-Crespo and Agnew 1992, R. L. Pitman, unpubl. data
San Félix, San Ambrosio	hundreds–perhaps several thousand (100)	0	Jun 1970; breeding on both islands	Jehl 1973, unpubl. data; Bahamonde 1974

are not distinct. No consistent differences in bare-part coloration (Table 3) or plumage (see below) differentiate the three YB populations. Similarly, there were no significant differences in size among males, and in females the only difference was that Chilean birds had larger wings than Mexican birds ($F = 10.168$, $P < 0.001$). In neither sex did DFA indicate any consistent differences in size or shape among these three YB populations (Table 4, Fig. 2).

Orange-billed boobies.—Orange-billed boobies nests by the tens of thousands in the Galápagos Archipelago and Malpelo Island, in much smaller numbers on Isla La Plata, and in only token numbers on the islands of Clipperton and San Benedicto, and possibly Alijos Rocks (Table 2, Fig. 1). All turn-of-the-cen-

TABLE 3. Soft part coloration of *Sula granti* and *S. dactylatra*.

Race (locality)	Coloration: Iris	Coloration: Bill	Coloration: Legs and feet	Reference
S. granti				
(Galápagos)	orange	rosy pink in females; more orange in males	olive or khaki in males; lead or olive in females	Nelson 1978
(Malpelo)	orangish	pinkish-orange, more yellow toward tip	yellowish-olive in males; blue-gray with hint of magenta in females	R. L. Pitman, unpubl. data
(San Benedicto)		deep orange	gray	Howell and Webb 1990
(Clipperton)	orangish	orange-pink	blue-gray or greenish-yellow	R. L. Pitman, unpubl. data
S. d. californica				
(San Benedicto)	yellow	bright yellow to greenish-yellow	pale green with blue tinge or olive with yellow tinge; webs paler	R. L. Pitman and J. Jehl, unpubl. data
S. d. Chile				
(San Félix and San Ambrosio)	yellow	yellow to greenish-yellow	khaki yellow, light olive, or greenish	J. Jehl, unpubl. data
S. d. personata				
(Kure)		bright yellow, brighter in breeding males	olive drab to bluish-gray	Kepler 1968
(New Zealand)		yellowish	greenish-blue	Oliver 1930
(W. Australia and Indian Ocean)	yellow to yellowish gray; brighter in males	yellow in males; yellowish-gray in females	dull olive in males; lead-gray in females	Marchant and Higgins 1990
S. d. bedouti				
(Bedout, Australia)			blue	Mathews 1913
S. d. fullagari				
(Lord Howe, Norfolk, Kermadecs)	sepia	buff yellow	varied grayish; feet and webs dull chrome yellow	O'Brien and Davies 1990
			greenish-gray	Oliver 1930
S. d. dactylatra				
(Ascension)		straw	dull orange (range from rich orange in some males to dull olive in some females)	Dorward 1962
S. d. melanops				
(Red Sea, Indian Ocean)	yellow	orange-yellow to yellow-green	lead gray	Brown et al. 1982

TABLE 4. Loadings on discriminant function axes based on five morphological measurements for three yellow-billed populations (*Sula dactylatra* "*californica*", *S. d. personata*, and *S. d.* "Chile") and one orange-billed population (*S. granti*). Data are for males only.

Variable	Axis 1	Axis 2	Axis 3
Bill length	0.078	0.390	0.058
Bill depth	0.795	−0.679	0.104
Wing	−0.425	−0.103	−0.756
Tail	−0.140	0.429	1.083
Tarsus	0.506	0.755	−0.395
Canonical correlation	0.701	0.374	0.101
% Variance explained	76.8	19.6	3.6

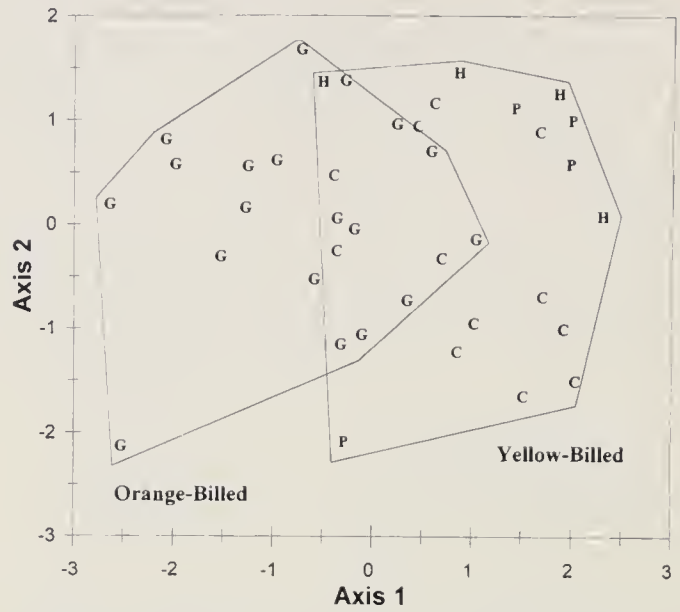

FIG. 2. Discriminant function analysis on morphological measures of four populations of "Masked" boobies (males only). Letters indicate population identity of specimens: (C) *Sula dactylatra* californica; (H) *S. d.* "Chile"; (P) *S. d. personata*; (G) *S. granti*. Polygons circumscribe yellow- and orange-billed forms.

tury ornithologists who visited both Clipperton Island and the Galápagos recognized their distinctiveness. Although similar to YB boobies (Frontispiece), they differ in size and proportions, as first noted by Snodgrass and Heller (1902) and Gifford (1913).

In contrast to comparisons among YB populations, our quantitative comparisons between YB and OB populations indicate that OB birds are distinct. Univariate comparisons indicated that OB birds have a significantly shallower bill ($F = 9.129$, $P < 0.04$ for males from all populations; $F = 5.478$, $P < 0.01$ for *S. d. personata* females), thinner bill ($F = 7.361$, $P < 0.03$ for males from *S. d. californica* and *S. d. personata*; $F = 6.125$, $P < 0.02$ for females from *S. d. californica* and *S. d. personata*), longer wing ($F = 10.168$, $P < 0.001$ for female *S. d. californica* only), and shorter legs ($F = 6.483$, $P < 0.01$ for male *S. d.* "Chile"; $F = 5.906$, $P < 0.01$ for female *S. d.* "Chile"). Discriminant function analysis showed that OB birds are generally smaller, having shallower bills, shorter tarsi, and longer wings (Table 4, Fig. 2). The smaller size of OB birds is further indicated by body mass, which averages 12–14% lighter than *S. d. personata* (Anderson 1993). They are also more sexually dimorphic in bill, wing, and tarsus than YB boobies (Fig. 3).

Plumage.—The full plumage sequence in boobies remains to be worked out. Because Masked Boobies do not breed until age 3–4 years (E. A. Schreiber, pers. comm.), they probably require several years to attain the definitive black-and-white adult plumage. Since a similar range of variation occurs in both OB and YB forms, we presume that the sequence of plumages develops on about the same schedule.

Despite some variation with each plumage type (age group?), there are consistent differences between OB and YB birds (Figs. 4, 5). In juvenile OB birds the dorsal areas are grayish brown, as compared to dark chocolate to blackish. Also, the upper back is usually dark, lightening with age; if a white collar is present it is narrow or incomplete. In YB birds the upper back is white, usually forming a broad and conspicuous collar. In OB birds feathers on the head and neck tend to be uniform grayish brown with diffuse flecking; in YB birds they are darker brown and appear blotchy. In addition, the central rectrices in OB birds tend to be pale at the base, as if dusted with flour, and the extent increasing with age, so that some older sub-adults appear white-rumped; in YB populations the rectrices average darker, and whitish bases, if present, are usually concealed by the upper tail coverts. In definitive plumage, OB and YB forms are similar, except that the dark areas tend to be

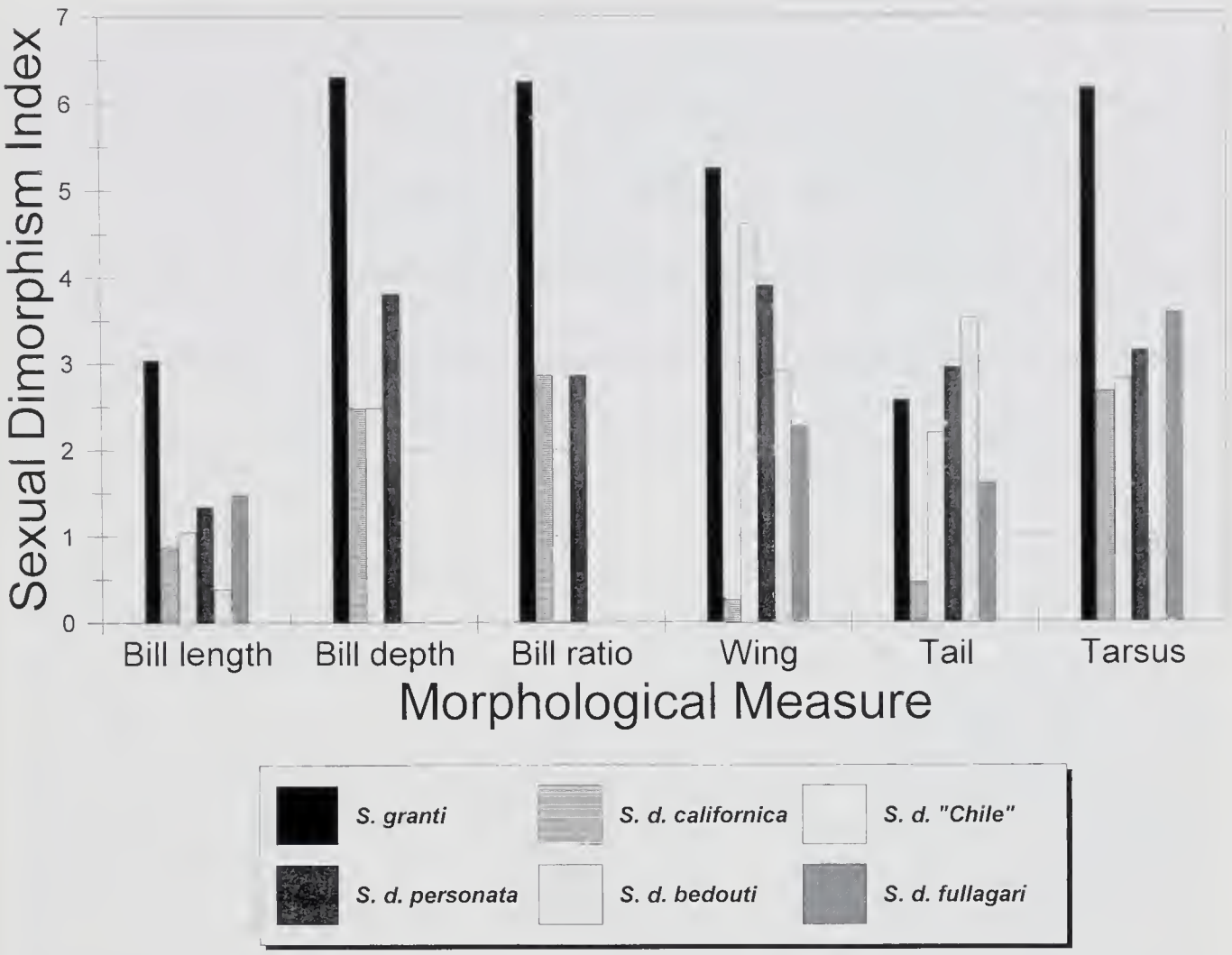

FIG. 3. Indices of sexual dimorphism among populations of "Masked" boobies calculated as: |male − female|/male × 100.

a rich chocolate brown with a reddish tinge in OB birds, compared to dark brown to blackish in YB birds, and the central rectrices average paler and may be almost entirely white, a condition that is rare in all YB populations.

Biology.—Several biological characteristics also differentiate OB and YB boobies. The first is that they pair assortatively on breeding islands. Although we could not analyze it statistically because often only one adult was present at the nest during the day, RLP observed only positive assortative pairing in colonies where both forms occur. Specific counts of OB birds include up to eight mated pairs on San Benedicto Island in November 1990, single roosting pairs on Roca Partida in August 1987 and August 1989, and at least six different pairs at Clipperton Island in May 1987 and November 1990 (Table 2). Considering that there are currently over 60,000 YB birds on Clipperton as compared to 150 OB, the presence of OB—but not mixed—pairs is further evidence of mate preference. Furthermore, both forms have apparently nested at Clipperton at least since the turn of the century (Beck 1907, Sachet 1962, this study), evidently with little or no interbreeding as parental forms still predominate there. Moreover, RLP observed no mixed pairs in any colony, although he did note two birds with intermediate-colored bills, one at San Benedicto on 14 March 1988, and another, paired with a YB, on Clipperton on 5 May 1987, suggesting that some hybridization may occur. There was an observation of a possible mixed pair on Clipperton in 1901 (Beck 1907) and a definite mixed pair on San Benedicto in 1988 (Howell and Webb 1990).

A second difference is preferred nesting habitat. In our experience YB birds use flat, open terrain, such as Clipperton Island, the Chilean islands, and the flat top of San

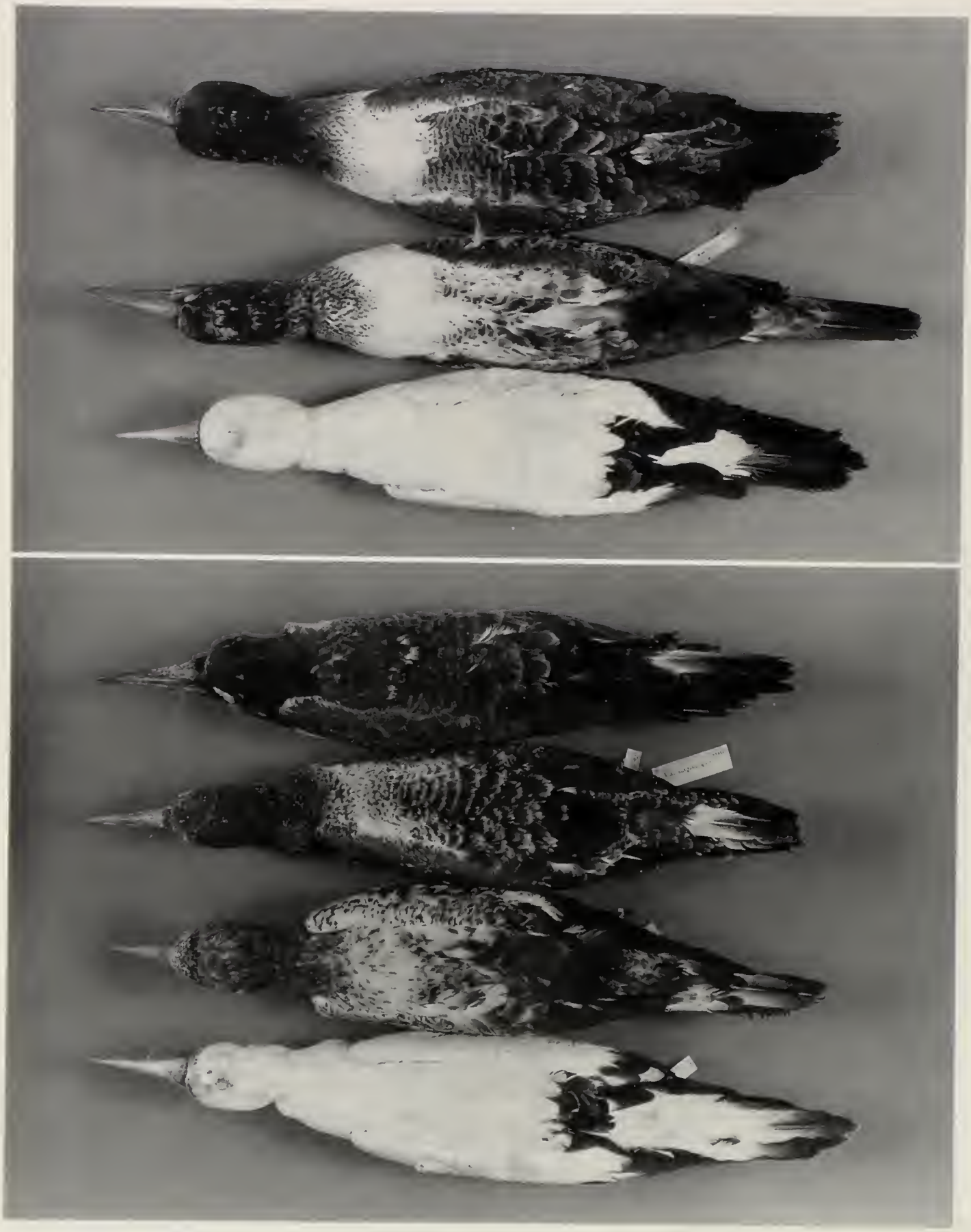

FIG. 4. Dorsal view of plumage sequences in yellow-billed (top) and orange-billed (bottom) "Masked" boobies. Above, top to bottom: *Sula dactylatra personata*, ANMH nos. 18900, 18899, 18901; below, top to bottom: *S. granti*, AMNH nos. 729,234, 729,238, 720,338, and 407,818.

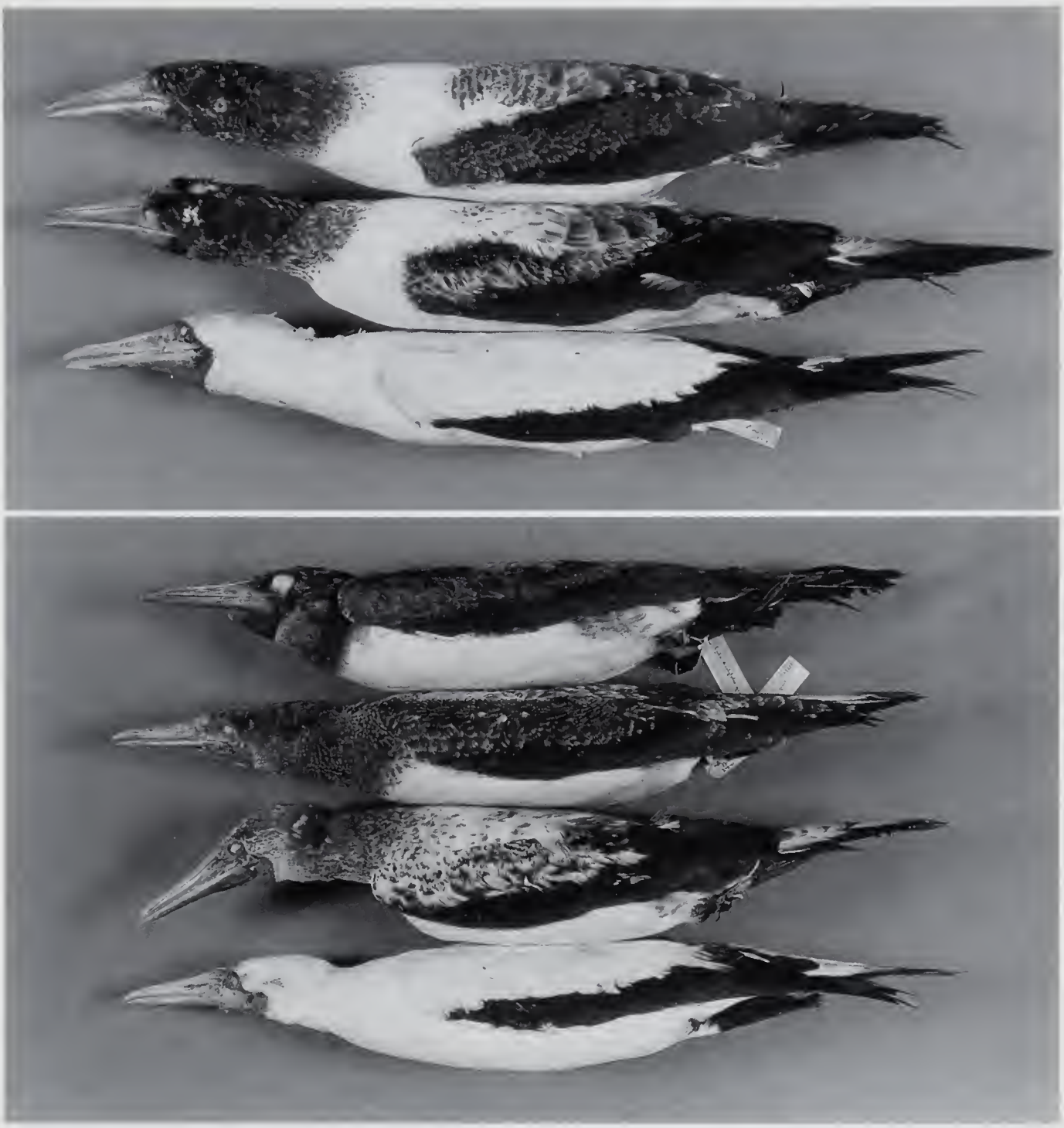

FIG. 5. Lateral view of plumage sequences in yellow-billed (top) and orange-billed (bottom) "Masked" boobies; specimens as in Figure 4.

Benedicto Island, whereas OB birds nest on steep cliffs of high islands like Malpelo, and Wenman and Culpepper, the northernmost Galápagos islands (Fig. 6; Nelson 1978, Duffy 1984, Gibbs et al. 1987). The difference was particularly evident at San Benedicto, where nearly all YB boobies nested on the flat upper surface of the island (mostly on the floor and around the flat rim of Herrera Crater), while the small OB colony (about 25 birds) was on the edge of a sloping cliff and at least 150 m from the nearest nesting YB individuals. The same preferences extend to roosting habitat. At Roca Partida, a tiny rock formed by two nearly vertical peaks that each rise 30 m above the sea with a low saddle joining them, YB birds roosted only on the flat saddle, where-

FIG. 6. A comparison of breeding habitats on (a) Clipperton Island, where over 60,000 *Sula dactylatra* breed, and (b) Malpelo Island, home to 24,000 *S. granti* (hundreds of nesting boobies are visible only as white dots in this photo). Photos by R. L. Pitman.

as OB birds roosted (and possibly nested: Howell and Webb 1990) only on the sides of the peaks. Duffy (1984) suggested that OB birds in the Galápagos preferentially nest near cliff edges because they may have problems taking flight from flat areas.

Finally, the two forms have different pelagic realms. YB boobies north of the equator tended to concentrate around, and to the west of, the Clipperton/Revillagigedos colonies (Fig. 7a), whereas OB boobies, including at least some banded individuals from the Galápagos, move northward from Galápagos/Malpelo to an area off Middle America (Anderson 1993), where they concentrate along the coast from Colima, Mexico, southward to Ecuador (Fig. 7b). Recent observations by RLP indicate that they also occur in small numbers throughout Gulf of California. The pelagic range of the Chilean birds is conjectural. YB birds south of the equator in Figure 7a are possibly of central Pacific (see Pitman 1986) or Chilean origin. Jehl (1973) observed occasional Masked Boobies, presumably from Islas Desventuradas, up to 200 km to the southeast.

DISCUSSION

Yellow-billed Masked Boobies in the eastern Pacific are geographically variable, being smallest in the north (*S. d. "californica"*; Clipperton and Mexican islands) and largest in the south (Chile). However, the differences are not statistically significant, and are within the range of variation of the geographically intermediate populations in the central Pacific. Thus, only one YB race, *S. d. personata,* can be recognized in this general area, and its relationship to the other named Masked Booby populations awaits review. The OB booby, on the other hand, differs from all YB populations in so many ways that we consider it to comprise a distinct species, *Sula granti.* These differences include mate preference, breeding habitat, and oceanic range that would be relevant to a biological species definition; as well as size, shape, degree of sexual dimorphism, bill color, and plumage pattern, which would support distinctiveness under a morphological species concept.

Bare-part coloration is an important distinguishing character of sulids in general (Nelson 1978) and Masked Boobies are no exception: the orange bill of *S. granti* separates it from all other forms of *S. dactylatra* (Table 3). At sea, adult *S. granti* and many juveniles are readily separable from YB forms by bill color alone (Howell and Engel 1993; RLP, pers. obs.). Even in long-dried museum specimens, the bill color of adult *S. granti* is usually apparent. This difference likely promotes species recognition. Foot color, despite its historical use in characterizing the various subspecies, has never been adequately described (Nelson 1978) and its taxonomic significance, as questioned by Murphy (1936), will only be resolved after seasonal, sexual, ontogenetic, and geographic factors are considered. Sex differences, at least, are involved: when RLP visited Malpelo Island in November, 1987, he could readily sex *S. granti* (verified by vocalizations: Nelson 1978) based on foot color alone (Table 3).

Pitman (1986) presented at-sea sightings data for over 10,000 Masked Boobies from the eastern tropical Pacific collected on cruises that occurred mainly during the first half of the year. At that time he did not distinguish between OB and YB boobies and the results showed a widespread distribution with no obvious pattern, except for dense concentrations within daily foraging ranges of the main colonies. Subsequent observations, however, in which the two forms were differentiated, although limited to the second half of the year, show that both forms prefer highly productive waters but in different areas (Figs. 7a, b). The concentration of OB boobies off southern Mexico (see also Anderson 1993, Howell and Engel 1993) corresponds to an area of seasonally strong, coastal upwelling off the Gulf of Tehuantepec (Blackburn 1962, 1963). The northern YB boobies concentrated along the 10° N latitude west of Clipperton Island, which corresponds to the northern boundary of the Northern Equatorial Countercurrent, a particularly rich feeding area for higher vertebrates (Wyrtki 1966, Reilly 1990). The significance of these habitat preferences is suggested by the fact that the Gulf of Tehuantepec is actually closer to Clipperton than it is to Galápagos or Malpelo; nevertheless, Clipperton boobies apparently prefer to forage farther offshore.

Evidence of reproductive isolation between *S. granti* and *S. dactylatra* is provided by ob-

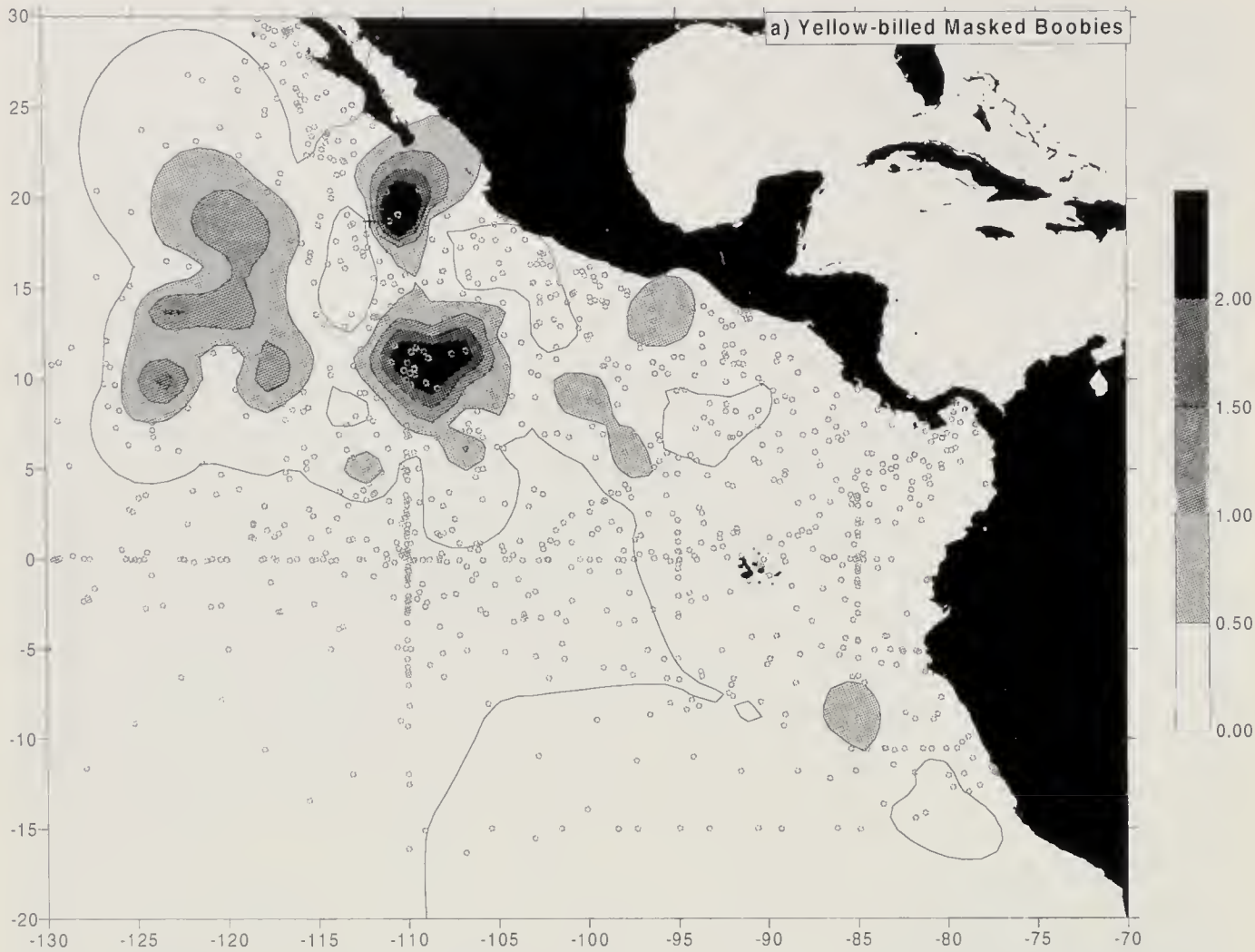

FIG. 7. Pelagic ranges of (a) yellow-billed (*Sula dactylatra*) and (b) orange-billed (*S. granti*) "Masked" boobies in the eastern Pacific identified on the basis of bill color. The average number of individuals of each form seen per hour is calculated for each 2° block of longitude and latitude in which they were recorded and the results contoured using Surfer (Keckler 1995). Noon ship positions for days when no bird was seen is indicated by an open circle. Sample sizes: OB = 701, YB = 243 (Pitman, unpubl. data).

servations of positive assortative mating within colonies where they occur together. Genetic analyses that extend our knowledge of booby evolution will be of great interest, as will observations that clarify any isolating mechanisms that allow these forms to avoid interbreeding. Also of interest are the selective forces that have modified body shape and increased sexual dimorphism of *S. granti* versus *S. dactylatra*. The increased dimorphism may be related to the fact that Galápagos is the only place in the world where "Masked" and Blue-footed (*S. nebouxii*) boobies breed sympatrically. Blue-foots are highly sexually dimorphic and substantially smaller than any of the YB populations [average mass of Blue-foot females is 1801 g, males 1283 g (Nelson 1978)]. In the Galápagos, Blue-foots feed mainly on sardines (*Sardinops sagax*; Anderson 1989), whereas YB boobies throughout the tropics feed mainly on flyingfish (Anderson 1993). During most years *S. granti* in the Galápagos feed mainly on sardines, but they can successfully switch to flyingfish during El Niño years when the sardines are unavailable and the Blue-foots starve (Anderson 1989). Perhaps *S. granti* is smaller and more sexually dimorphic than YB boobies because it has converged on Blue-footed Booby ecologically and morphologically as an adaptation to prey availability and variability within the Galápagos environment (see Boersma 1978).

Snow and Nelson (1984) pointed out that the Galápagos has the highest incidence of seabird endemism of any island group in the world and our study indicates that the otherwise pantropical Masked Booby has not been exempted from the modifying influence of

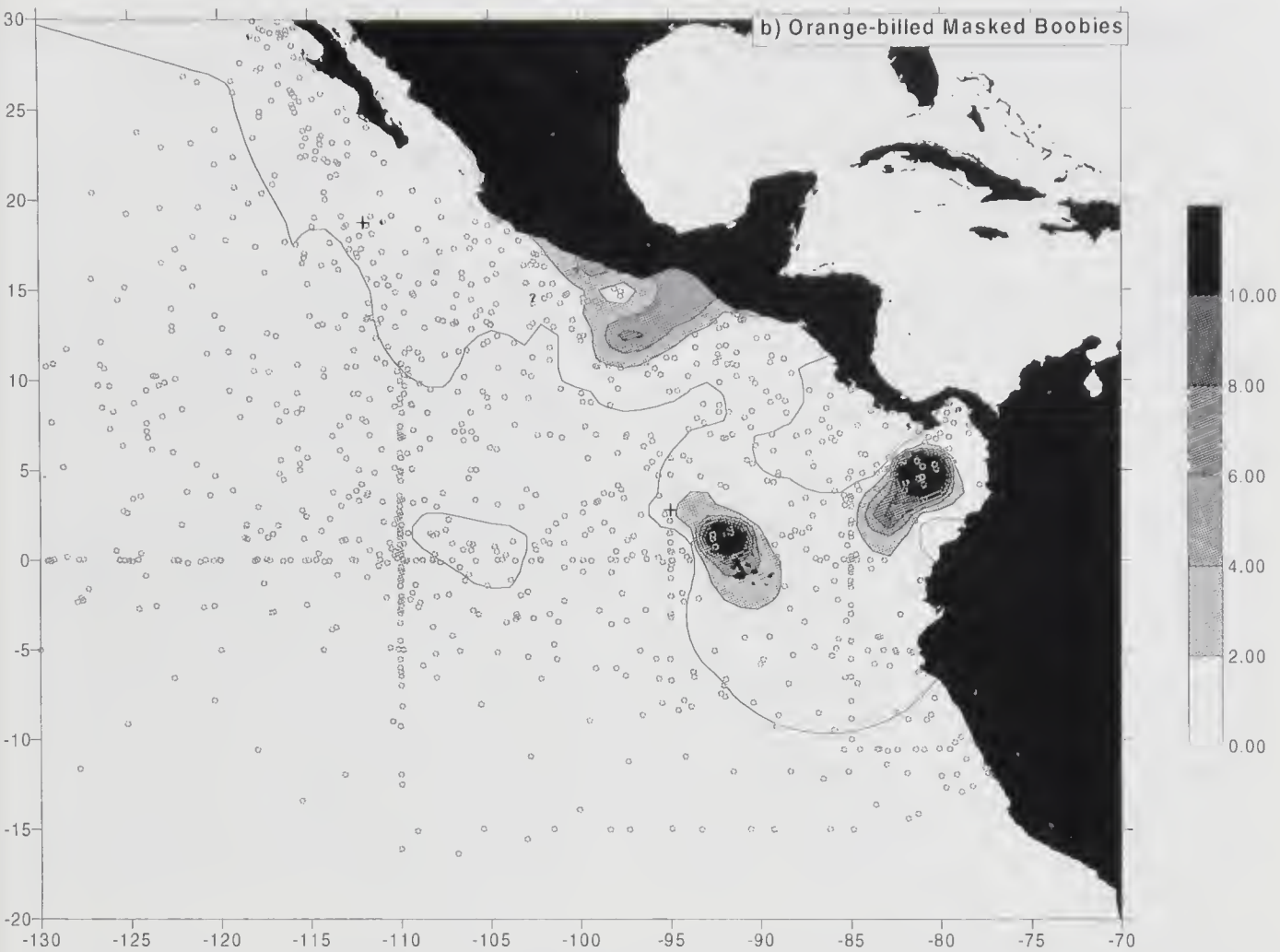

FIG. 7. Continued.

that environment. As a common name for *Sula granti* we propose Nazca Booby, which recognizes that the current breeding range and probably evolutionary history of this species is closely associated with the Nazca Crustal Plate.

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Wilson Bull., 110(2), 1998, pp. 171–181

SEASONAL NUMBERS AND DISTRIBUTION OF SHOREBIRDS ON NORTH CAROLINA'S OUTER BANKS

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ABSTRACT.—We documented the seasonal abundance, distribution, and relative importance of outer beach habitats to shorebirds on the Outer Banks of North Carolina. The Outer Banks span 228 km and attract millions of tourists every year, underscoring the need for baseline data for conservation. Twenty-one species were recorded during the study. The most abundant were Sanderling (*Calidris alba*), Red Knot (*Calidris canutus*), and Willet (*Catoptrophorus semipalmatus*). As an assemblage, shorebirds were most abundant in May and August. Peak numbers for each species were recorded between April–May and July–September. The greatest numbers were recorded on North Beach and the lowest on South Beach (1992) and Bodie Island (1993). Shorebird abundance was greater during fall (68 birds/km) than in spring (50 birds/km). Patterns of abundance of the eight most abundant species were examined in detail. Black-bellied Plovers (*Pluvialis squatarola*), Willets, Whimbrels (*Numenius phaeopus*), Ruddy Turnstones (*Arenaria interpres*) and Sanderlings were most abundant on North Beach. North Core Banks harbored the highest numbers of Piping Plovers (*Charadrius melodus*), American Oystercatchers (*Haematopus palliatus*), and Red Knots. American Oystercatchers and Whimbrels were significantly more abundant during spring than fall, whereas Willet and Sanderlings were more abundant during fall. The Outer Banks emerged as an important staging area for the Atlantic populations of Piping Plovers, Whimbrels, and Sanderlings when compared to 7 other areas along the eastern U.S. coast. The importance of the area to Sanderlings was reaffirmed by return rates of 58%, most (69–89%) returning to the beach stretch where they were banded. The area gains special significance because it also supports a nesting population of Piping Plovers. Our findings confirm that the Outer Banks of North Carolina provide a critical link in the migratory path of several shorebird species. Habitat loss or alteration could adversely affect the Atlantic Flyway population of several species (e.g., Sanderlings) as well as the threatened Piping Plover. *Received 1 May 1997, accepted 13 Jan. 1998.*

Many migrant shorebirds rely on a few, key stopover sites to complete their annual migratory cycle (Myers et al. 1987). These sites often provide a unique combination of food resources and habitat necessary to support a large number of birds (Myers 1986, Myers et al. 1987). Examples of important sites in North America are Delaware Bay (Clark et al. 1993), the Bay of Fundy (Hicklin 1987), the Copper River Delta of Alaska (Isleib 1979, Senner 1979), and Grays Harbor in Oregon (Senner and Howe 1984). Because a large proportion of a species' population may be concentrated at one or a few sites during migration, shorebirds are particularly vulnerable to habitat loss and degradation, and thus to population decline (see Gill and Handel 1990). Coastal areas, where the vast majority of these key sites occur, are seriously threatened by habitat alteration and destruction by human development (Senner and Howe 1984, Davidson and Pienkowski 1987). Survey information for additional or alternative sites is lacking, mostly because resources to implement adequate survey programs have not been available (Senner and Howe 1984). Such information is needed in the event of losses of key sites.

The Outer Banks of North Carolina constitute a prime example of a potentially important area for which only limited information on migratory shorebirds is available (Buckley and Buckley 1973, Root 1988, Senner and Howe 1984, Boone 1988). Previous information was gathered as part of short-term surveys and Christmas Bird Counts. From these efforts, it was estimated that 20,000 shorebirds used the Outer Banks annually during autumn. At least 15 species of shorebirds used the Outer Banks during winter. Abundant spe-

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cies included Black-bellied Plover (*Pluvialis squatarola*), Willet (*Catoptrophorus semipalmatus*), Red Knot (*Calidris canutus*), Sanderling (*Calidris alba*), Dunlin (*Calidris alpina*), and Short-billed Dowitcher (*Limnodromus griseus*). These data, while informative, were limited in that they did not rest on geographically extensive, replicated surveys. Because the area is subject to ever increasing development and tourism pressures (Parnell et al. 1992), broader, replicated surveys are needed to better assess the importance of the Outer Banks and potential impacts caused by human use.

Here we present geographically extensive data on the monthly and seasonal numbers and distribution of shorebirds using outer beach habitats in the Outer Banks collected during 1992 and 1993. Information on the shorebird community as a whole, and the eight most abundant species is emphasized. Special attention is given to the following species of concern: Piping Plovers (*Charadrius melodus*), Whimbrels (*Numenius phaeopus*), Red Knots, and Sanderlings. Conservation needs of these species are heightened because of their threatened status (Piping Plover), recent population declines (Whimbrel and Sanderling; Howe et al. 1989), or their localized distribution along the Atlantic Flyway (Red Knot; Morrison and Harrington 1992). We also assessed the relative regional importance of the Outer Banks for these species by comparing peak counts from this study to those obtained through the International Shorebird Survey (ISS, Manomet Observatory for Conservation Science) for seven other sites along the Atlantic Flyway. We estimated Sanderling population size and turnover rates using mark-resight techniques (Dinsmore 1994). On the basis of observations of color-marked individuals we present distribution and site fidelity patterns for this species.

STUDY AREA AND METHODS

The Outer Banks are located along the east-central coast of North Carolina (34° 34′–35° 50′ N, 75° 27′–76° 39′ W; Fig. 1). The area consists of a series of narrow barrier islands with a length of approximately 228 km stretching from just north of Oregon Inlet in Dare County to Beaufort Inlet in Carteret County. Much of the area is included in Cape Hatteras and Cape Lookout National Seashores. Because of its inaccessibility, this study was restricted to the northern portions of the Outer Banks north of New Drum Inlet.

The topography is typical of barrier islands, with a low elevation and flat relief. Outer beach habitat occupied by shorebirds was sandy and devoid of vegetation. Outer beach is defined as the area from the base of the dune line to the ocean edge, including that portion of the intertidal zone exposed at low tide. Outer beach did not include soundside tidal flats at inlets or other tidal flat habitats. Mean tidal amplitude is approximately 1 m.

Censuses.—From March 1992 to December 1993, five sites ranging from 9–34 km in length were surveyed. These sites were chosen mostly for accessibility, but were representative of outer beach habitat within the study area. Bodie Island (9 km) extended from the south edge of Nags Head south to Oregon Inlet. North Beach (28 km) extended from the Rodanthe pier south to a point 1 km north of the Buxton town limit. South Beach (24 km) extended from just south of the Cape Hatteras lighthouse south to Cape Hatteras point, then west to Hatteras Inlet. Ocracoke Island (28 km) included the entire island from Hatteras Inlet south to Ocracoke Inlet. North Core Banks (34 km) included the entire island from Ocracoke Inlet south to New Drum Inlet. The total amount of outer beach surveyed monthly for shorebirds was 123 km. Additionally, a stretch of Pea Island National Wildlife Refuge (19 km) extending from the Oregon Inlet jetty south to Rodanthe was censused during the fall 1993 season.

Surveys were conducted twice per month by vehicle. All surveys were begun 1.5 h before low tide, except for two counts on North Core Banks in July and August 1992 that were begun 1.5 h before high tide. Numbers and species of all shorebirds present on the outer beach were recorded. Flying birds were not recorded, unless they were clearly disturbed by the investigators. Because large shorebird concentrations (> 500 birds) were rare, data here represent actual counts and not estimates.

Abundance was first calculated as the mean of the two monthly censuses for each site to minimize variance problems associated with repeated measures within a month (Hurlbert 1984). For a few sites, there was only one count in a given month and this was treated as the estimate for that month. We report patterns of abundance in two ways: monthly numbers (mean number of shorebirds per month) and seasonal numbers (sum of the mean monthly counts within a season). We also used a factorial ANOVA to test for seasonal patterns in abundance (JMP 1994). In this model, seasons were defined as spring (April–June) and fall (July–November). All statistical analyses were performed using JMP v. 3.1.5 software on a Macintosh computer (JMP 1994). These seasons span the major migration periods for the species examined (Dinsmore 1994). The effects of site and year on the variability of monthly counts were tested. Month, a repeated measure, was nested within seasons. To meet homogeneity of variance requirements, data were log or square root transformed. The most appropriate transformation was determined

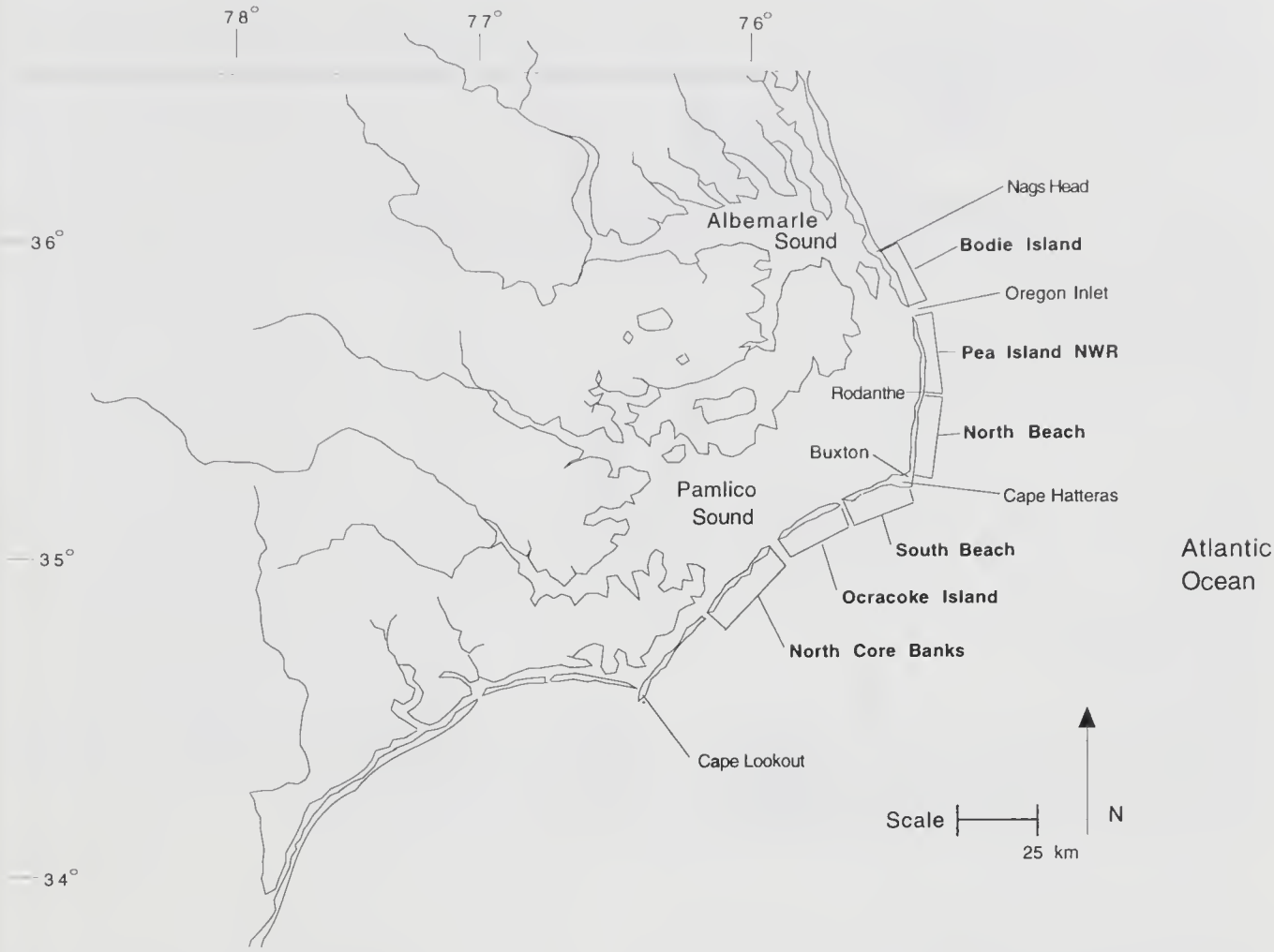

FIG. 1. Map of the Outer Banks of North Carolina showing barrier islands and locations visited between March 1992 and December 1993.

by examining plots of residuals. Abundance, expressed as birds/km, of the eight selected shorebird species was also calculated for each site.

Peak fall counts of Piping Plovers, Whimbrels, Red Knots, and Sanderlings obtained during this study were compared to similar counts obtained at seven other sites, excluding Delaware Bay, along the Atlantic Coast and the Gulf Coast of Florida. Counts were obtained from International Shorebird Survey (ISS) data for the fall migration period (July to November) in 1972–1992. Only marine sites surveyed over at least nine years were used for these comparisons. Censuses at ISS sites were generally conducted at 10-day intervals, but sampling effort was sometimes variable. Thus, the peak count of each species was treated as the estimate for the site (see Colwell and Cooper 1993). Counts obtained during this study were ranked with counts for the other seven sites to assess the importance of the Outer Banks to each of these species.

Distribution and site fidelity of Sanderlings.—To examine the seasonal distribution and site fidelity of Sanderlings, birds were color-marked during 1992–1993. Sanderlings were caught primarily with a rocket net, although some were initially caught in mist nets. Most birds were caught at roost sites where they were herded in front of the rocket net for capture. A few were caught as they concentrated at foraging areas along the outer beach. Because of seasonal changes in distribution, Sanderlings were trapped at North Core Banks in spring and at four sites on Cape Hatteras National Seashore during fall (Dinsmore 1994). Trapping was conducted from 28 April–27 May and 29 July–16 October in 1992 and from 22 April–23 May and 27 July–4 November in 1993. Birds were removed from the net immediately after capture and transferred to cardboard holding boxes. All birds were fitted with an aluminum U. S. Fish and Wildlife Service leg band and a series of either four (1992) or three (1993) color bands arranged in a unique combination. The color bands were U.V. stable PVC bands (A. C. Hughes, London, England). Combinations were derived from six and ten possible colors during 1992 and 1993, respectively. Color band seams were sealed to reduce the possibility of band loss. Birds were released at the capture site within three hours of capture.

Marked birds were surveyed from a four-wheel drive vehicle every 5–7 days. During surveys, complete and partial color band combinations were recorded, as well as the number of unmarked birds examined for color bands. Very large (> 500 birds) concentrations of sanderlings were rare, which increased the ease of examining birds for color bands.

TABLE 1. Seasonal means (± SE), seasonal totals and month of peak count of shorebirds on the Outer Banks of North Carolina, 1992–1993. Seasonal numbers are means of the monthly counts within each season; peaks are given by month with the number recorded in parentheses.

Species[a]	Seasonal means[b]		Seasonal totals[c]		Month of peak count
	Spring	Fall	Spring	Fall	
All species	5684 ± 2421	7760 ± 1118	17,051	38,798	May (11,540)
Black-bellied Plover	194 ± 113	282 ± 76	582	1408	October (472)
Wilson's Plover	2 ± 1	1 ± 1	6	7	May, July, August (3)
Semipalmated Plover	28 ± 27	27 ± 10	82	134	May (81)
Piping Plover	13 ± 2	31 ± 9	39	155	September (58)
American Oystercatcher	114 ± 22	79 ± 26	342	397	July (152)
Willet	369 ± 52	1034 ± 452	1108	5168	July (2750)
Whimbrel	175 ± 150	100 ± 60	526	500	May (474)
Marbled Godwit	0	2 ± 1	0	8	October (4)
Ruddy Turnstone	176 ± 125	116 ± 58	527	581	May (419)
Red Knot	1363 ± 725	267 ± 27	4088	1334	May (2764)
Sanderling	3222 ± 1796	5692 ± 907	9667	28,458	August (8194)
Semipalmated Sandpiper	21 ± 18	24 ± 13	63	120	September (70)
Western Sandpiper	1 ± 1	17 ± 8	4	84	September (43)
Least Sandpiper	2 ± 2	5 ± 4	5	26	September (19)
Dunlin	1 ± 1	53 ± 38	4	263	November (196)
Short-billed Dowitcher	1 ± 1	29 ± 22	4	146	July (117)

[a] Five species were recorded < 5 times (Killdeer, Greater Yellowlegs, Lesser Yellowlegs, Spotted Sandpiper, and White-rumped Sandpiper).
[b] Seasons are defined as Spring (April–June) and Fall (July–November).
[c] The sum of the monthly means over the season.

The inter-annual site fidelity (i.e., return rates) of Sanderlings was examined by looking at 1993 resightings of birds banded in 1992 at North Core Banks, Bodie Island, and North Beach. Only birds resighted after April 1, 1993 were used because most overwinter mortality should have occurred by then. Resighting probabilities were assumed to be equal among sites. Birds resighted at more than 1 location in 1993 (n = 117) were excluded from this analysis. A χ^2 test for homogeneity of resightings by location was computed for each of the three locations. The observed values for each of the three sites were calculated by determining the number of birds marked at a given site (e.g., site A) and resighted at sites A, B,and C. The same calculations were made for birds marked at sites B and C. The expected value for each test was then the sum of the marked birds seen at each site divided by the number of sites. In each case, the denominator was 3, and the test had 2 degrees of freedom.

The within-season site-fidelity of Sanderlings was examined during fall 1993. During that season, birds were marked at Bodie Island, Pea Island, North Beach, and South Beach. Resighting efforts were conducted on all sites except North Core Banks. Only birds resighted at least once in each of two different capture periods were used in this analysis. A bird was considered site-faithful if at least two-thirds of the resightings were from the banding site. The percentage of birds that were faithful to their banding site are reported by banding location.

RESULTS

Shorebird assemblage.—Twenty-one species were recorded on surveys (Table 1). Species richness was slightly greater in fall (21 species) than in spring (18 species). Totals of 52,651 shorebirds in 1992 and 58,935 shorebirds in 1993 were recorded. Surveys revealed that Sanderling, Red Knot, and Willet were the most abundant shorebird species and accounted for 89% of the total numbers. Sanderlings were the single most abundant species and accounted for 68% of the total (Table 1).

Shorebirds were present on the Outer Banks throughout the study, although numbers peaked during May and from July to September in fall. The fewest were recorded during June ($F = 4.93$, d.f. = 12, 46; $P < 0.001$; Fig. 2). Shorebird numbers varied between sites and seasons ($F = 2.84$, d.f. = 4, 46; $P = 0.03$). Shorebirds were most abundant on North Beach during both years, and least abundant on South Beach during 1992 and on Bodie Island during 1993. On all sites except Ocracoke Island and North Core Banks, shorebird numbers were highest during the fall season. Abundance of shorebirds was

FIG. 2. Numbers of the shorebird community (ALLSP), Black-bellied Plovers (BBPL), Piping Plovers (PIPL), American Oystercatchers (AMOY), Whimbrels (WHIM), Ruddy Turnstones (RUTU), Red Knots (REKN), and Sanderlings (SAND) and Willets (WILL) detected on beach censuses on the Outer Banks of North Carolina, March 1992–December 1993.

greater in fall (68 birds/km) than in spring (50 birds/km), with a peak at North Beach during fall (117 birds/km; Table 2). Spring passage was rapid, being confined almost entirely to the month of May, whereas in fall, birds began arriving in July and some lingered into November or even December (Fig. 2).

Black-bellied Plover.—Black-bellied Plovers were present every month of the year, although the greatest numbers were recorded in May and August–October. The lowest numbers were recorded from January to March. Spring migrants arrived in April, peaked in May, and were gone by early June. Fall migrants began arriving in August, peaked in October, and most departed by November ($F = 5.74$, d.f.: 12, 46; $P < 0.01$; Fig. 2). Very few birds overwintered. Population sizes did not vary by site or season. Plovers were most abundant on North Core Banks (27% of total) and North Beach (32% of total). Abundance was quite low at all sites, being greatest at North Beach during fall (4 birds/km; Table 2).

Piping Plover.—Piping Plovers were recorded every month of the year, with the greatest numbers recorded July–October.

TABLE 2. Abundance (birds/km) of eight shorebird species by season at five sites on the Outer Banks of North Carolina, 1992–1993. Mean count/site (all sites considered) by season is listed in the last column. Spring = S, Fall = F. Sites shown in Figure 1.

	Bodie Island		North Beach		South Beach		Ocracoke		N. Core Banks		Mean/site	
	S	F	S	F	S	F	S	F	S	F	S	F
All shorebirds	59	88	31	117	36	41	49	36	74	56	50	68
Black-bellied Plover	3	2	2	4	2	2	2	1	2	3	2	2
Piping Plover	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
Am. Oystercatcher	<1	1	<1	<1	2	1	1	<1	1	1	<1	<1
Willet	2	6	3	12	2	6	4	9	5	9	3	8
Whimbrel	7	1	3	2	1	<1	<1	<1	<1	<1	2	<1
Ruddy Turnstone	2	1	1	2	3	2	<1	<1	2	<1	2	1
Red Knot	3	1	<1	<1	1	<1	16	1	34	6	11	2
Sanderling	44	76	23	97	26	28	26	22	29	34	30	51

Numbers from April to June were stable. Very few were recorded during January and February. Spring migrants arrived in March with a slight peak in April. About 40 pairs remained and bred during the summer. Fall migrants arrived in July, peaked in August and September, and most departed by November. A few birds overwintered. There were no significant differences between months within season and year ($F = 1.00$, d.f.: 24, 46; $P > 0.05$; Fig. 2). Numbers varied significantly between sites ($F = 3.01$, d.f.: 4, 46; $P = 0.03$); most (69%) occurred on North Core Banks. Numbers did not vary between seasons. Compared to other ISS sites, the Outer Banks ranked second in regional importance to this species (Table 3). Only Monomoy National Wildlife Refuge in Massachusetts had a higher peak count than the Outer Banks. Bird abundance was very low (<1 bird/km) at all sites (Table 2).

American Oystercatcher.—American Oystercatchers were recorded mostly from March to December, with almost none present in January and February. Numbers peaked from May to August. Spring birds arrived in March, with stable counts from May to August indicating breeding birds. Most birds departed in September, with a few remaining into November ($F = 3.36$, d.f.: 12, 46; $P < 0.01$; Fig. 2). Numbers varied significantly by site and season ($F = 3.36$, d.f.: 4, 46; $P = 0.02$). Oystercatchers were most abundant on North Core Banks (31% of total) and South Beach (33% of total). At North Core Banks and Ocracoke Island, numbers were greatest during spring. Numbers at the other three sites were higher during fall. Abundance was low at all sites, being greatest at South Beach during spring (2 birds/km; Table 2).

Willet.—Willets were recorded every month of the year, although the greatest numbers were recorded in July and August. Otherwise, numbers were quite stable from April to December, with slightly fewer birds present from January to March. Spring migrants ar-

TABLE 3. Peak numbers of four shorebird species at eight sites along the Atlantic Coast and Gulf Coast of Florida from International Shorebird Survey data (Manomet Observatory for Conservation Sciences) and at the North Carolina Outer Banks (1992–1993).

Site	Piping Plover	Whimbrel	Red Knot	Sanderling
Plymouth Beach, MA	57	19	950	2500
Monomoy NWR, MA	100	585	3000	5000
Jamaica Bay NWR, NY	0	10	1685	350
Great Egg Harbor, NJ	23	33	2294	1400
Chincoteague NWR, VA	50	355	2175	11,130
Outer Banks, NC	91	453	600	11,257
Cape Romano, FL	25	7	8115	809
Marco River, FL	24	3	1211	457

rived in April, peaked in May, with some remaining into June to breed. During fall, the peak was in July, with smaller numbers remaining through December (F = 7.43, d.f.: 12, 46; $P < 0.01$; Fig. 2). Numbers varied significantly by site and season (F = 2.70, d.f.: 4, 46; $P = 0.04$). Willets were most abundant on North Core Banks (26% of total) and North Beach (29% of total). At all sites, Willets were more numerous during fall. They were three times more abundant in fall than spring at North Beach and Bodie Island. Abundance was much greater in fall (8 birds/km) than spring (3 birds/km) with the greatest abundance recorded at North Beach during fall (12 birds/km; Table 2).

Whimbrel.—Whimbrels were recorded mostly from April to September, with distinct peaks in May and in July and August. None was recorded from December to March. Spring migrants arrived in April, peaked in May, and very few remained in June. Fall migrants arrived in July, peaked in July and August, and nearly all had departed by September with a few lingering to November (F = 15.63, d.f.: 12, 46; $P < 0.01$; Fig. 2). Whimbrel were most abundant on North Beach (42% of total) and Bodie Island (24% of total). Numbers increased significantly in 1993 (F = 5.50, d.f.: 1, 46; $P = 0.02$) for all sites except North Core Banks. There was also significant variation between seasons (F = 7.10, d.f.: 1, 46; $P = 0.01$). Whimbrels were slightly more abundant in spring. Compared to other ISS sites, the Outer Banks ranked second in regional importance to this species (Table 3). Monomoy National Wildlife Refuge in Massachusetts was the only site to have a higher peak count. Abundance was low at all sites except Bodie Island where the peak was recorded during fall (7 birds/km; Table 2).

Ruddy Turnstone.—Ruddy Turnstones were present every month of the year, although the majority were present from May to June and from August to September. Numbers were lowest from January to April. Spring migrants arrived in April, showed a strong peak in May, and most departed by June. Fall migrants arrived in July, peaked in August, and most departed by October (F = 11.49, d.f.: 12, 46; $P < 0.01$; Fig. 2). Ruddy Turnstones were most abundant on South Beach (33% of total) and North Beach (30% of total), although site differences were not significant. Abundance was low at all sites with the peak at South Beach during spring (3 birds/km; Table 2).

Red Knot.—Red Knots were present every month of the year, although the greatest numbers were recorded in May and June. Numbers from July to December were fairly stable, with the lowest numbers recorded from January to March. Spring migrants arrived in April, peaked in May, and most departed by June. During fall, birds arrived in July, showed a small peak in September, and moderate numbers were still present in November (F = 2.87, d.f.: 12, 46; $P < 0.01$; Fig. 2). Numbers varied significantly between sites (F = 5.62, d.f.: 4, 46; $P < 0.01$). Most Red Knots were seen at North Core Banks (65% of total) and Ocracoke Island (28% of total). Compared to other ISS sites, the Outer Banks ranked last in regional importance to this species (Table 3). Abundance was much higher in spring (11 birds/km) than in fall (2 birds/km), with most birds recorded at North Core Banks (34 birds/km) and Ocracoke Island (16 birds/km; Table 2).

Sanderling.—Sanderlings were present every month of the year, although the greatest numbers were present in May and from July to October. The lowest numbers were recorded in March and June. Spring migrants arrived in April, peaked in May, and most departed by June. Fall migrants arrived in July, peaked in August and September, and steadily decreased throughout November (F = 4.19, d.f.: 12, 46; $P < 0.01$; Fig. 2). Sanderlings were most abundant on North Beach (41% of total) and North Core Banks (20% of total), although site differences were not significant. Compared to other ISS sites, the Outer Banks ranked first in regional importance to this species (Table 3). Sanderling abundance was much greater in fall (51 birds/km) than in spring (30 birds/km; Table 2). Spring birds peaked on Bodie Island (44 birds/km) while fall birds peaked on North Beach (97 birds/km).

Sanderlings exhibited moderate within-season site fidelity. Most (i.e., 50–62%) remained faithful to the area in which they were banded during the fall 1993 migration (Table 4). Others usually moved to an adjacent site, less than 10 km away in most cases. Sanderlings showed high inter-annual site fidelity. Fifty-

TABLE 4. Percentage of resightings of Sanderlings on the Outer Banks of North Carolina by banding site during fall 1993. The percentage of Sanderlings resighted in at least 2 sites are also reported. Banding sites are shown in Figure 1.

	Resighting sites						
Banding site	Bodie Island	Pea Island	North Beach	South Beach	Ocracoke Island	2 sites	>2 sites
Bodie Island	62.6	8.0	1.1	0	0	26.2	2.1
Pea Island	7.5	52.5	7.5	2.5	0	25.0	5.0
North Beach	2.9	2.6	52.2	11.9	1.1	27.0	2.3
South Beach	0	0	6.3	50.0	0	12.5	31.2

eight percent (380/655) of the birds marked during 1992 were resighted in 1993. A significant proportion of the birds returned to their banding site. The proportions returning were 0.89 for North Core Banks ($\chi^2 = 102.9$, $P < 0.01$), 0.82 for Bodie Island ($\chi^2 = 174.7$, $P < 0.01$), and 0.69 for North Beach ($\chi^2 = 74.2$, $P < 0.01$).

DISCUSSION

The 21 species detected in this study were representative of shorebirds commonly found on barrier island beaches along the Atlantic Coast (Senner and Howe 1984). Sanderling was the most abundant species, followed by Red Knot and Willet. The patterns of abundance contrast markedly with those at Delaware Bay, one of the most important stopovers for shorebirds along the Atlantic Coast (Myers 1983). At Delaware Bay, Semipalmated Sandpiper was the most abundant species, followed by Ruddy Turnstones, Red Knots, and Sanderlings (Clark et al. 1993). Differences in abundance between these sites likely are due to the differences in habitats surveyed. In this study we focused on outer beach habitat, while the Delaware Bay study included other habitats such as beaches adjacent to tidal flats and salt marshes (Clark et al. 1993).

The high number of Piping Plovers using the Outer Banks indicates the importance of the area to this federally threatened species. In addition to supporting a breeding population of approximately 40 pairs (Collazo et al. 1995), the area is an important staging site, especially in fall. We recorded a peak of 89 individuals during September 1992, most on North Core Banks. However, single-day counts of 128 on 29 August 1992, 110 on 25 September 1992, and 136 on 20 August 1993 on North Core Banks were made independently of censuses. These counts included large numbers of plovers using tidal flats at Ocracoke and New Drum inlets. North Core Banks is probably one of the most important staging areas for the Atlantic Coast population of Piping Plovers (see Haig and Plissner 1993). The 1991 International Piping Plover Census recorded 1975 adult plovers along the Atlantic Coast of Canada and the United States (Haig and Plissner 1993). Based on these numbers and assuming no turnover, a minimum of 7% of the Atlantic Coast population of Piping Plovers uses North Core Banks during migration.

Moderate numbers of Red Knots use the Outer Banks during migration and in winter. Morrison and Harrington (1992) estimated the North American population of Red Knots at 180,000. The vast majority of these birds stage in Delaware Bay during spring (Clark et al. 1993), with small concentrations noted at other sites along the Atlantic Coast (Hicklin 1987, Marsh and Wilkinson 1991). On the Outer Banks, more than 4700 knots were counted in May and June 1992, most (73%) on North Core Banks. Not accounting for turnover, our peak count of 2764 individuals (Table 1) indicates the Outer Banks host a minimum of 1–2% of the estimated North American Red Knot population during spring. The importance of the Outer Banks as a wintering area is poorly understood. Censuses indicated that over 500 knots wintered each year, the northernmost sizeable wintering aggregation on the Atlantic Coast. The largest known wintering group in North America is on the Gulf Coast of Florida, where a mean of 6300 (± 3400 S.E.) were detected in 1980–82 (Harrington et al. 1988). In South Carolina, no sizeable winter concentrations of knots were noted in the Cape Romain-Santee Delta

region (Marsh and Wilkinson 1991). The Outer Banks may also be important as a stopover for migrant Whimbrel. Large numbers also use the Cape Romain-Santee Delta region of South Carolina (Marsh and Wilkinson 1991), resulting in single-day counts of over 400 in April and over 200 in August. Information about other critical staging areas for this species is scant.

Sanderlings were the most abundant species. Their abundance was similar to those reported by Walters (1984) for fall (50 birds/km) but not for spring (175 birds/km). Comparative data for the Atlantic Coast is limited to Delaware Bay in New Jersey, a site of hemispheric importance to this species (> 200,000 during migration; Myers et al. 1990). Concentrations of up to 30,000 birds/km have been reported at this site. Other comparative data come from the Pacific Coast. From California to Washington, concentrations of 40 birds/km were reported in winter (Myers et al. 1984). Concentrations of 185 birds/km were reported in coastal Oregon and Washington during spring, with a peak of 472 birds/km at Clatsop Beach, Oregon in early May (Myers et al. 1984). Myers and coworkers (1988) reported abundances of 46, 41, and 22 birds/km in California during fall, winter, and spring, respectively. The lower abundance on the Outer Banks compared to western sites might be attributed to poorer habitat quality. Alternatively, the extent of outer beach habitat in North Carolina may be greater than in coastal California (see Connors et al. 1981, Myers et al. 1984), resulting in fewer birds/km.

Sanderlings tended to be sedentary during migration periods. Most (mean = 54%) remained at their banding site during a given season. This figure may actually underestimate site-fidelity, because birds that moved short distances between sites were not counted as site-faithful. For example, North Beach and South Beach were adjacent to each other, and small numbers of Sanderlings fed on North Beach but roosted on the nearest portion of South Beach. Such individuals were not considered site-faithful because they moved between census areas. Our results indicate that individual Sanderlings are somewhat mobile, but most ranged less than 10 kilometers from their banding site.

Distributional patterns may result from differential food availability between sites. Sanderlings were most abundant on North Beach and North Core Banks, which collectively hosted more than 60% of all individuals counted. Observations of food items (n > 1000) captured by Sanderlings and limited work on food availability suggest that Sanderlings prey almost exclusively on mole crabs (*Emerita talpoida*) along the beaches of the Outer Banks (Dinsmore 1994). This is consistent with other sites where Sanderlings and mole crabs co-occur (Myers et al. 1980, Connors et al. 1981, Maron and Myers 1985). Comparisons between North Beach (high Sanderling abundance) and Ocracoke Island (low Sanderling abundance) indicate that the abundance of mole crabs was significantly higher on North Beach (Dinsmore 1994).

Variations in food supply are thought to influence seasonal variation in Sanderling numbers in North Carolina (Walters 1984). At Pea Island National Wildlife Refuge, Dolan and coworkers (1993) reported that mole crab numbers peaked in May–July and in October. Few were detected from December–March. This pattern of mole crab abundance matches the seasonal trends in the numbers of Sanderlings on the Outer Banks (Dinsmore 1994). Sanderlings quickly increase in late July and early August and remain somewhat stable through October. After October, Sanderlings depart from the Outer Banks. The late fall exodus of Sanderlings is a pattern not found in California, where Sanderling numbers remain fairly stable from early October until they begin to decline in February (Myers 1980). It is likely that Sanderlings remain on the Outer Banks as long as possible, departing only when the food supply diminishes. The drastic reduction in mole crab numbers after October may explain the drop in Sanderling (and perhaps other species) numbers in November.

Because the Outer Banks ranked as the site with the highest peak count during fall migration when compared to seven other sites along the Atlantic Coast, it appears to be an important staging area for Sanderlings. Delaware Bay in New Jersey is the only site to record higher peak counts than those on the Outer Banks. The importance of the Outer Banks to migrant Sanderlings becomes clearer when turnover is considered. An estimated 35–

40,000 Sanderlings use the Outer Banks annually, most during fall migration (Dinsmore 1994). These data suggest that the Outer Banks are an area of regional importance to Sanderlings under the guidelines of the Western Hemisphere Shorebird Reserve Network (i.e., supporting 20–40,000 birds annually during migration, Myers et al. 1987). The dependency of many migrant Sanderlings on the Outer Banks is confirmed by the strong interannual site fidelity reported in this study. The 1993 return rate of Sanderlings banded on the Outer Banks in 1992 was 58%. Philopatry of Sanderlings has been reported in other studies (Evans et al. 1980; Myers 1988; Myers et al. 1988, 1990; Summers et al. 1987). At Bodega Bay, California, the annual return rate of Sanderlings was 72% for adults and 50% for first-winter birds (Myers 1980). Our findings confirm that the Outer Banks of North Carolina provide a critical link in the migratory path of several shorebird species (e.g., Sanderling, Whimbrel). If habitat loss or alteration were to occur, portions of their Atlantic Flyway populations could be negatively affected, perhaps contributing to further population decline (Howe et al. 1989). The threatened Piping Plover, which depends on the Outer Banks for breeding habitat, could also be affected by such habitat changes. Given the regional significance of this area, efforts to ensure the continued availability of habitat for shorebirds amidst demands for development and recreational uses should constitute a conservation priority.

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ENVIRONMENTAL CORRELATES OF DIURNAL AND NOCTURNAL FORAGING PATTERNS OF NONBREEDING SHOREBIRDS

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ABSTRACT.—Knowledge of abiotic factors influencing the foraging ecology of nonbreeding shorebirds (Charadriiformes: Charadrii) is based on research conducted almost exclusively during the day. Consequently, we examined the relative contributions of environmental variables to diurnal and nocturnal foraging patterns (presence/absence) of nonbreeding shorebirds at Humboldt Bay, California, USA from January 1992 to January 1993. The influence of environmental variables on foraging patterns differed between day and night. Most notably, the diurnal presence of birds increased with: (1) shorter daylength [Black-bellied Plover (*Pluvialis squatarola*), dowitchers (*Limnodromus* spp.), and small sandpipers (*Calidris mauri* and *C. minutilla*)]; and (2) shorter durations of mud flat exposure [American Avocet (*Recurvirostra americana*), Marbled Godwit (*Limosa fedoa*), and Dunlin (*Calidris alpina*)]. By contrast, the nocturnal presence of most species increased during the fall [Marbled Godwit, dowitchers, Black-bellied Plover, Semipalmated Plover (*Charadrius semipalmatus*), and Dunlin] and on nights with a visible moon [Marbled Godwit, Willet (*Catoptrophorus semipalmatus*), dowitchers, Semipalmated Plover, and Dunlin]. Our results suggest that interspecific variation in diurnal and nocturnal feeding patterns of shorebirds is associated mostly with variation in tidal, seasonal, and moonlight conditions. Furthermore, our findings suggest that nocturnal foraging by most shorebird species at a northern temperate, intertidal site did not increase during periods of short daylength. *Received 28 July 1997, accepted 13 Jan. 1998.*

Nonbreeding distributions of shorebirds in coastal habitats are influenced by numerous environmental factors, especially tides and weather (see Burger 1984), which influence the availability of food resources. Tides predictably alter the amount of available foraging habitat, and variation in temperature, wind, and daylength further influence the availability of intertidal prey (Evans 1976). These generalizations, however, are based largely on research conducted during the day despite the growing body of literature (e.g., McNeil 1991, Dodd and Colwell 1996, McNeil and Rodríguez S. 1996) documenting nocturnal foraging by shorebirds. Consequently, the environmental correlates of nocturnal foraging by shorebirds remain poorly understood.

Only one study (Robert et al. 1989) has quantified environmental influences of both diurnal and nocturnal distributions of shorebirds. Most studies (e.g., Heppleston 1971, Zwarts et al. 1990, Evans and Harris 1994, Thibault and McNeil 1994) have evaluated the contributions of one environmental factor (moonlight) to nocturnal foraging by shorebirds. Furthermore, with the exception of Robert and coworkers (1989) and Zwarts and coworkers (1990), most researchers have focused on a single species. Findings from these studies suggest that the nocturnal foraging ecology of shorebirds is influenced by variation in tides (Robert et al. 1989), moonlight (Heppleston 1971, Robert et al. 1989, Zwarts et al. 1990, Evans and Harris 1994, Thibault and McNeil 1994), and season (Rompré and McNeil 1994, Dodd and Colwell 1996).

In this paper, we examine the relative contributions of environmental variables to diurnal and nocturnal foraging by eight shorebird species at Humboldt Bay, California, USA, an important Pacific Coast estuary for nonbreeding shorebirds (Colwell 1994). Elsewhere (Dodd and Colwell 1996), we showed that shorebirds at North Humboldt Bay foraged principally during the day, although diurnal and nocturnal distributions varied both among seasons and species.

STUDY AREA AND METHODS

We studied shorebirds (Charadriiformes: Charadrii) from 10 January 1992–10 January 1993 at the Arcata Marsh Project in North Humboldt Bay, Humboldt Co., California, USA. North Humboldt Bay is the largest of three basins comprising Humboldt Bay with approximately 12.2 km^2 of exposed tidal mud flat at mean low tide (Costa and Stork 1984). Local tides are

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mixed semidiurnal. The climate is characterized by a wet (November–March) and a dry (April–October) season, although we conducted our study during mostly drought conditions when yearly rainfall was 19.5 cm below normal (National Weather Service, Eureka, CA). For further details concerning the study area see Gerstenberg (1979) and Barnhart and coworkers (1992).

Bird censuses.—We established four 20 × 50 m study plots (marked with four 5 × 5 cm wooden corner stakes) on a high elevation mud flat (Gerstenberg 1979) within 50 m of the shoreline in areas of high shorebird use. Each week, we censused each plot twice within a 24-hour period: once during daylight and once during darkness on successive rising tides. We censused during rising tides because shorebirds foraged along the advancing tide edge eventually congregating near the shoreline, which allowed close observation. We censused only one plot within a 24-hour period. Within each week, we randomly chose a 24-hour period in which to census a plot from 24-hour periods that had tides of sufficient magnitude so the water reached the plot both in darkness and in daylight. We conducted each census for 45 minutes beginning when the edge of the rising tide crossed the corner stake of a plot. For further details concerning sampling see Dodd and Colwell (1996).

We observed birds with binoculars from a vehicle parked 21–51 m away on dikes. We arrived at observation points at least 30 minutes before a census to minimize disturbance to birds. At night, we verified observations by briefly (3–5 seconds) illuminating plots with a 400,000 candlepower spotlight (Black Max Q-beam, Brinkmann Corp., Dallas, TX) covered with a red or amber snap-on filter [see Dodd and Colwell (1996) for further details]. We illuminated plots immediately after we had recorded data on species, abundance, and behavior of birds (not presented in this paper). Additionally, we illuminated plots whenever we (1) heard, but could not see, shorebird(s) or (2) had not detected shorebirds for 5–7 min. Finally, we recorded the presence of shorebirds on four areas (area 1 = 1.8 ha, area 2 = 3.7 ha, area 3 = 1.5 ha, area 4 = 2.3 ha) encompassing plots to evaluate whether or not data from plots were representative of surrounding mud flats (Dodd 1995).

At night, we had difficulty identifying some closely related species. Consequently, we combined observations of Western and Least sandpipers (*Calidris mauri* and *C. minutilla*, respectively) into the group "small sandpipers" and Long-billed and Short-billed dowitchers (*Limnodromus scolopaceus* and *L. griseus*, respectively) into the group "dowitchers". Hereafter, we treat these groups as if they were species.

Environmental variables.—For each census, we recorded season, moonlight, tide, daylength, and weather variables.

We categorized (*a priori*) censuses by season based on migratory patterns of shorebirds in the Humboldt Bay area (Gerstenberg 1979, Harris 1991) as: (1) fall: 1 July–30 November (n = 85); (2) winter: 1 December–17 March (n = 50); (3) spring: 18 March–8 May (n = 29); and (4) summer: 9 May–30 June (n = 22).

We recorded the phase of the moon in tenths (from 0 = a new moon to 10 = a full moon) based on United States Naval Observatory data (Tidelogs 1992, 1993); we did not distinguish between waxing and waning moons. At night, we recorded whether or not the moon was visible during any portion of a census.

We recorded the following based on National Oceanic and Atmospheric Administration data (Tidelogs 1992, 1993): (1) height (m) of low tide preceding a census tide; and (2) time (minutes) from low tide to a census tide.

We used the amount of time (minutes) between sunrise and sunset of the 24 hour census period (Tidelogs 1992, 1993) to represent daylength. In addition, we used the amount of time (minutes) between sunrise and sunset of the 24 hour census period in which tides occurred below 1.2 m (Tidelogs 1992, 1993) as an index of the duration of mud flat exposure during daylight (hereafter, referred to as available daylength). At 1.2 m, high elevation mud flats of North Humboldt Bay are usually just inundated by an advancing tide (Dodd, pers. obs.). Our index, however, did not account for variations from predicted tides caused by weather conditions such as strong onshore winds or heavy rainfall.

We categorized precipitation that occurred during a census as: (1) absent, (2) fog, or (3) rain; and the degree of cloud cover that prevailed for most of a census as: (1) ≤ 10%, (2) 11–75%, and (3) > 75%. We used the following data from the National Weather Service's daily record of surface weather observations for Eureka, California as an index of conditions at the study area (5.8 air-km away): (1) wind speed (km/h); (2) wind direction (eight compass points); and (3) air temperature (° C).

Data summary and analysis.—We restricted analyses to the eight most common species, including only observations from fall, winter, and spring because few shorebirds occurred during summer (Dodd 1995). Additionally, we omitted from analyses July–September censuses (n = 51) for Dunlin (*Calidris alpina*) because this species is a late fall migrant and usually does not arrive at Humboldt Bay until late September (Dodd, pers. obs.). We analyzed plot data for all species, with the exception of American Avocet (*Recurvirostra americana*) for which we analyzed area data because data from plots did not represent the surrounding the mud flat (Dodd 1995).

We evaluated the relative contributions of environmental variables to day and night foraging patterns of shorebirds using stepwise forward logistic regression (Hintze 1992; see also Hosmer and Lemeshow 1989) with a χ^2 cutoff value of 2.7 (df = 1, $P < 0.10$; e.g., Johnson and Temple 1990). All analyses were performed on an IBM-compatible computer using NCSS, ver. 5.3 software (Hintze 1992). We used stepwise regression because it is effective for screening many covariates, especially when little is known about the response variable (i.e., nocturnal foraging; Hosmer and

Lemeshow 1989). For each species, we conducted separate day and night analyses using presence or absence of foraging birds as the response variable and environmental variables as independent variables.

We examined all covariates for multicollinearity (high intercorrelations among independent variables) by regressing each independent variable against all others and evaluating the coefficient of determination (R^2; Hamilton 1992). We concluded that the following variables exhibited high intercorrelations ($R^2 > 0.60$): (1) daylength (day = 0.68, night = 0.76); (2) available daylength (day = 0.73, night = 0.91); (3) tide height at low water (day = 0.78, night = 0.86); and (4) amount of time since low water (day = 0.68, night = 0.62). Indeed, when the stepwise procedure selected more than one of these variables, it produced extremely high estimated standard errors and/or a reversal of one or more beta coefficient's signs, both indications of multicollinearity (Hamilton 1992). Consequently, for models fitted with more than one intercorrelated variable (day: four of eight, night: three of eight), we excluded from analyses three of the four intercorrelated variables (Hamilton 1992). For each model, we kept the intercorrelated variable with the highest χ^2 value based on univariate logistic regression.

Finally, we encountered a numerical problem of complete separation (Hosmer and Lemeshow 1989) associated with the analysis of Marbled Godwit (*Limosa fedoa*). Because this species occurred on plots at night exclusively during fall, complete discrimination between fall and the other seasons occurred, resulting in no possible maximum likelihood estimate and correspondingly high standard errors (Hosmer and Lemeshow 1989). To remedy this, we randomly added to plot data 1 of 2 winter occurrences and 1 of 17 fall occurrences from nights when Marbled Godwit foraged on areas, but not on plots (Dodd 1995).

RESULTS

Season contributed significantly to nocturnal use of mud flats by shorebirds (Table 1). For five of eight species, presence at night increased during fall. Moreover, fall contributed most (i.e., lowest *P*-value; see Hosmer and Lemeshow 1989) to nocturnal foraging patterns of Marbled Godwit, Black-bellied Plover (*Pluvialis squatarola*), and Semipalmated Plover (*Charadrius semipalmatus*). By contrast, season correlated significantly with diurnal feeding patterns of only two species: the diurnal presence of Semipalmated Plover and Willet (*Catoptrophorus semipalmatus*) increased and decreased, respectively during fall.

Moon variables contributed significantly to both day and night use of mud flats, but in different ways. At night, the presence of five of eight species increased on nights with a visible moon. In addition, moonlight contributed most to nocturnal foraging patterns of Willet, Dunlin, and dowitchers. During the day, we did not record the visibility of the moon; however, the phase of the moon correlated significantly with diurnal use of mud flats. The presence of dowitchers, Dunlin, and small sandpipers increased on days closest to a new moon.

Tidal variables contributed significantly to foraging patterns of a few species, but correlations differed between day and night. During the day, the presence of Dunlin increased when higher, low tides preceded censuses and the presence of American Avocet and Marbled Godwit increased when less time had elapsed since low tide. By contrast, the nocturnal presence of dowitchers and Dunlin increased when lower low tides preceded censuses. Overall, tidal factors influenced diurnal use more than nocturnal use. Shorter durations of exposed mud flat contributed most to diurnal foraging patterns of American Avocet, Marbled Godwit, and Dunlin.

During both the day (Black-bellied Plover, dowitchers, and small sandpipers) and night (American Avocet and small sandpipers), the presence of birds increased with shorter daylength or available daylength. However, the nocturnal presence of Willet increased with longer daylength. Short daylength or available daylength contributed most to diurnal use of mud flats by Black-bellied Plover, dowitchers, and small sandpipers, and nocturnal use by American Avocet.

Weather variables influenced day and/or night foraging patterns of most species. Correlations of temperature and windspeed differed between day and night. During the day, presence of birds increased at lower temperatures (Marbled Godwit) and windspeeds (dowitchers and Dunlin), whereas at night, presence of birds increased at higher temperatures (Dunlin) and windspeeds (Marbled Godwit). However, the presence of birds both during the day (Marbled Godwit and Willet) and night (dowitchers, Dunlin, and small sandpipers) increased with precipitation. Moreover, rain contributed most to the nocturnal foraging presence of small sandpipers. Wind direction correlated with diurnal (American Avocet and Willet) and nocturnal (Marbled Godwit, Willet, and dowitchers) use of

TABLE 1. Results of stepwise forward logistic regression examining the relationship between diurnal and nocturnal foraging patterns (presence/absence) of eight shorebird species and environmental variables.

Species	Day/ night	Variables selected	Beta coefficient	Standard error	χ^2	P	% Corr. class[a]	% Present[b]
American Avocet[c]	Day	Time since low tide[e]	−0.02	0.004	28.51	<0.001	80.4	76.7
		Southeast wind	−1.35	0.67	4.02	0.04		
	Night	Available daylength[e]	−0.007	0.001	27.71	<0.001	74.1	56.2
Black-bellied Plover	Day	Daylength	−0.007	0.003	4.04	0.04	91.5	08.5
	Night	Season: fall	3.24	1.04	9.77	0.002	86.6	13.4
Semipalmated Plover	Day	Season: fall	2.22	1.07	4.35	0.04	93.9	06.1
	Night	Season: fall	1.62	0.66	5.99	0.01	89.6	10.4
		Moon visible	0.92	0.53	2.95	0.09		
Marbled Godwit	Day	Time since low tide[e]	−0.009	0.002	13.75	<0.001	72.6	61.0
		Temperature	−0.15	0.05	8.23	0.004		
		Fog	1.55	0.83	3.45	0.06		
	Night	Season: fall	3.74	1.32	8.02	0.005	92.7	07.9
		Moon visible	1.39	0.66	4.42	0.03		
		Windspeed	0.15	0.07	3.97	0.046		
		Southeast wind	1.52	0.76	4.02	0.045		
Willet	Day	Season: fall	−1.67	0.37	20.36	<0.001	70.7	38.4
		Fog	1.58	0.62	6.55	0.01		
		North wind	−1.08	0.58	3.48	0.06		
	Night	Moon visible	2.92	1.23	5.63	0.02	97.6	03.1
		Daylength[e]	0.01	0.006	4.51	0.03		
		East wind	2.16	1.13	3.67	0.055		
Dowitchers	Day	Daylength	−0.01	0.002	20.17	<0.001	76.8	34.7
		Moonphase	−0.14	0.06	4.91	0.03		
		Windspeed	−0.05	0.03	3.92	0.048		
	Night	Season: fall	4.42	1.31	11.33	<0.001	90.2	12.2
		Moon visible	2.88	0.74	15.04	<0.001		
		Fog	2.08	0.79	6.86	0.009		
		Northeast wind	4.86	2.19	4.92	0.03		
		Tide height at low water	−1.99	1.04	3.67	0.055		
Dunlin[d]	Day	Tide height at low water[e]	1.77	0.61	8.55	0.003	69.9	54.9
		Moonphase	−0.19	0.07	6.80	0.009		
		Windspeed	−0.06	0.03	3.65	0.056		
	Night	Moon visible	3.57	0.98	13.11	<0.001	86.7	15.9
		Rain	3.23	1.13	8.21	0.004		
		Season: fall	1.79	0.84	4.49	0.03		
		Partly cloudy	−1.75	1.04	2.84	0.09		
		Tide height at low water[e]	−2.33	1.23	3.60	0.06		
		Temperature	0.20	0.12	2.75	0.097		
Small sandpipers	Day	Available daylength[e]	−0.005	0.001	18.16	<0.001	67.7	48.8
		Moonphase	−0.09	0.05	2.85	0.09		
	Night	Rain	1.74	0.53	10.91	0.001	82.9	19.5
		Available daylength	−0.004	0.001	5.73	0.02		

[a] Percent of the total number of observations that were correctly classified using a classification midpoint of 0.5 (i.e., a species was predicted as absent (<0.5) when actually absent and present (>0.5) when actually present).
[b] Percent of censuses (n = 164) in which we observed a species foraging on a plot.
[c] Area data used instead of plot data; n = 163 (day), n = 162 (night) censuses.
[d] Early fall censuses (n = 51) excluded, leaving n = 113.
[e] Indicates one of four intercorrelated variables kept in analysis.

mud flats, but no generalities of wind direction resulted.

DISCUSSION

Our findings suggest that the presence of foraging shorebirds on intertidal mud flats of Humboldt Bay is influenced by a variety of environmental factors, and that these correlates vary among species (Table 1). During the day, tides and daylength contributed most to foraging patterns of shorebirds; bird use increased with shorter daylength (three species) and shorter periods of exposed mud flats (three species). By contrast, nocturnal foraging patterns correlated strongly with moonlight and seasonal variables; mud flat use by most species (five of eight) increased during fall and/or on nights with a visible moon.

We are aware of only one other study (Robert et al. 1989) that quantified environmental correlates (wind velocity, percent cloud cover, moonphase, and tide level) of both diurnal and nocturnal distributions of nonbreeding shorebirds. Robert and coworkers (1989) found that tide level best explained variation in both day and night abundance of foraging birds; abundance increased at low and intermediate tide levels for most species. Robert and coworkers conducted their study during winter, so they could not evaluate season or daylength variables.

Here and elsewhere (Dodd and Colwell 1996), we showed that nocturnal foraging by shorebirds of most species predominated during fall at Humboldt Bay. This pattern may be related to the biology of a species and environmental conditions that vary seasonally (Dodd and Colwell 1996) including: (1) high energy demands associated with migration and the pre-basic molt; (2) large numbers of immature birds, which may be inefficient foragers; (3) less available alternate foraging habitat (i.e., coastal pastures; Colwell and Dodd 1995); and (4) lower low fall tides occurring at night.

In addition to season, visibility of the moon correlated strongly with nocturnal foraging patterns. But interestingly, variation in moonphase did not correlate with nocturnal patterns of any species. Phase of the moon may not have been an important factor in our study because we conducted almost half (48%) of our night censuses when the moon was below the horizon. Excluding nights when the moon was below the horizon, shorebirds foraged on more (61.4%, n = 57) nights when the moon was more than half full than nights (39.3%, n = 28) when the moon was half full or less. We suggest that future studies quantify ambient moonlight as well as phase of the moon to evaluate the influence of moonlight on nocturnal foraging patterns.

Many researchers have reported a relationship between variation in moonlight and variation in nocturnal foraging by shorebirds. For example, Robert and coworkers (1989) showed that Wilson's (*Charadrius wilsonia*) and Semipalmated plovers foraged more on nights with a full moon than moonless nights, a pattern duplicated for territorial Whimbrel (*Numenius phaeopus*) and Willet (McNeil and Rompré 1995) foraging on moonlit versus moonless nights. Additionally, Eurasian Oystercatcher (*Haematopus ostralegus;* Heppleston 1971) and American Avocet (Evans and Harris 1994) occurred in higher numbers on moonlit nights than on dark nights. However, not all species conform to this pattern. Nocturnal distributions of Semipalmated Sandpiper (*Calidris pusilla*) varied independently of moonlight (Manseau and Ferron 1991), and densities of Little Stint (*Calidris minuta*) on dark nights exceeded densities on full moon nights (Zwarts et al. 1990). None of these studies evaluated both the phase and visibility of the moon.

The relationship between moonlight and nocturnal foraging by shorebirds has been argued to be associated with a species' foraging behavior (e.g., McNeil and Robert 1988, Robert et al. 1989). Presumably, birds that search for prey visually should be more influenced by variation in moonlight than birds that use tactile maneuvers to locate prey. However, in our study, this was not always the case. Nocturnal use of mud flats by typically visual foragers, such as plovers (Pienkowski 1981, 1983a, 1983b; McNeil and Robert 1988; Robert and McNeil 1989), either increased (Semipalmated Plover) or was not influenced (Black-bellied Plover) by a visible moon. Most Scolopacid species, both visual and tactile feeders (Pienkowski 1981, McNeil and Robert 1988, Robert and McNeil 1989), increased their use of mud flats on moonlit nights. By contrast, nocturnal distributions of

a predominately tactile feeder, American Avocet (Evans and Harris 1994), varied independently of moonlight. Elsewhere (Dodd and Colwell 1996), we showed that diurnal abundance exceeded nocturnal abundance for Scolopacids, whereas abundance of American Avocet and plovers did not differ between day and night. It is noteworthy that Scolopacids predominated during day censuses and tended to feed on moonlit nights. However, nocturnal distributions of small sandpipers varied independently of moonlight, as was found elsewhere (Manseau and Ferron 1991).

We did not evaluate the influence of moon visiblility on diurnal foraging patterns. However, diurnal use of mud flats by dowitchers, Dunlin, and small sandpipers increased on days closest to a new moon. Milsom (1984) reported that a greater proportion of Northern Lapwings (*Vanellus vanellus)* foraged during the day when more time elapsed to the next full moon. Several authors (Spencer 1953, Hale 1980, Milsom 1984, Barnard and Thompson 1985) have hypothesized that a negative relationship between diurnal feeding activity and moonphase indicates a preference by shorebirds to forage during nights with a full moon. However, Barnard and Thompson (1985) observed no foraging shorebirds on 11 nights with a full moon, despite the significant negative relationship they obtained between moonphase and the number of pastures used by lapwings during the day. The foraging ecology of shorebirds may be influenced by a lunar periodicity in invertebrate prey activity (e.g., Hale 1980, McNeil 1991, Thibault and McNeil 1994). Many marine invertebrates are known to be more active during full moons (Hale 1980, Ydenberg et al. 1984), although this is not the case for all invertebrates (e.g., Geppetii and Tongiorgi 1967, Zwarts 1990).

In marine habitats, tidal variation is considered the most important environmental factor influencing the abundance, distribution, and behavior of nonbreeding shorebirds (for review, see Burger 1984). In this study, we controlled most tidal variation by beginning censuses at the same tide height on rising tides. Despite this, tidal variation correlated with foraging patterns of some species and tidal influences seemed greater during the day than at night. Interestingly, the diurnal presence of birds increased with shorter durations of exposed mud flat, whereas the nocturnal presence of birds increased with longer durations of exposed mud flat. This difference may be attributed to diurnal and nocturnal variation in tides. At Humboldt Bay, diurnal and nocturnal tides typically are unequal in height, so that the lower low tide occurs during either daylight or darkness, depending on the season. For example, during fall, low tides averaged higher prior to day censuses than night censuses. Thus, birds foraging during the day tended to encounter relatively higher low tides than birds feeding at night, which may explain differences in day and night correlations of tide. Alternatively, differences would be explained if birds left mud flats earlier on rising diurnal tides than nocturnal tides. By contrast, other studies (Evans 1976, Hockey 1984, Manseau and Ferron 1991) have reported that shorebirds foraged for a shorter duration of the nocturnal tide cycle than diurnal tide cycle, with the exception of Turpie and Hockey (1993) who showed that shorebirds fed throughout the diurnal and nocturnal low tide period.

Numerous studies have shown that shorebirds spend more time foraging during the day in winter when foraging habitat is exposed for short durations of daylight (Goss-Custard 1969, Goss-Custard et al. 1977, Puttick 1979, Baker 1981, Pienkowski 1982, Maron and Myers 1985). At other northern temperate sites, nocturnal foraging by shorebirds is largely confined to winter (e.g., Goss-Custard 1969, Heppleston 1971, Pienkowski 1982). Other authors (Goss-Custard 1969, Goss-Custard et al. 1977, Evans 1988) have hypothesized that shorebirds at temperate latitudes are forced to feed at night in winter because high energetic requirements cannot be met during periods of short daylength. However, at Humboldt Bay, the nocturnal presence of only two species (American Avocet and small sandpipers) increased with shorter daylength, and the presence at night of Willet increased with longer daylength. Our findings suggest that most shorebird species at North Humboldt Bay do not have to forage at night when daylength is short.

Overall, weather variables were relatively unimportant correlates of both day and night foraging patterns. This may be due to the large-scale of both the response variable (i.e.,

presence/absence) and weather variables (i.e., we ignored microclimate). However, the presence of a few species increased with precipitation both during the day and night. Moreover, rain best explained the variation in nocturnal use of mud flats by small sandpipers. These results contradict findings from other studies (Goss-Custard 1970, Pienkowski 1981) which suggest that rain decreases the availability of invertebrate prey during the day.

Conclusions.—Our year-long study of shorebirds foraging on mud flats of North Humboldt Bay shows that environmental conditions associated with species' foraging patterns differed between day and night. Most notably, diurnal use of mud flats increased when intertidal habitats were exposed for shorter durations and daylength was short. By contrast, nocturnal use increased during fall, especially on nights with a visible moon. Finally and in contrast to other studies conducted at northern temperate sites, nocturnal foraging by most species did not increase during periods of short daylength. This finding suggests that most shorebirds wintering at Humboldt Bay are able to meet their energetic requirements during daylight.

We suggest that despite recent advances in our knowledge of nocturnal foraging by shorebirds, we do not understand the causes of the variation that occurs latitudinally, seasonally, and among species. Furthermore, we suggest that future studies examine influences of tidal, seasonal, and moonlight factors on diurnal/nocturnal patterns of shorebirds across a range of latitudes and taxa. Finally, findings from this study and Dodd and Colwell (1996) have important implications for how biologists determine the value of a particular site for nonbreeding shorebirds. In most cases, decisions on whether or not to protect an area are based on diurnal surveys. We urge researchers to evaluate both nocturnal and diurnal use of foraging habitats, especially during different seasons.

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EFFECTS OF FLUSHING NESTING GREATER PRAIRIE-CHICKENS IN ILLINOIS

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ABSTRACT.—Important reasons for evaluating researcher impact in nest studies include the possibility of increased abandonment, depredation, embryonic mortality, or bias of other parameters. From a 29-year data set of 1101 Greater Prairie-Chicken (*Tympanuchus cupido pinnatus*) nests in Illinois, we assessed the performance of 115 nests that were visited by investigators during egg laying or incubation. The minimum return rate for 107 hens flushed up to 5 times was 88% and apparently decreased ($G = 9.76$, df = 4, $P = 0.042$) with increased frequency of flushing caused by investigators. The success of 105 nests from which hens were flushed (68%) was higher ($G = 7.55$, df = 1, $P < 0.01$) than that of 840 undisturbed nests (53%) whose fates were determined prior to discovery. No desertions could be attributed to investigators activities. Embryonic mortality in disturbed nests appeared 3.7× higher ($Z = 4.59$, $P = 0.001$) than in undisturbed nests, but some egg removal by predators prior to our inspections may have biased results. Neither embryonic loss nor nest success was related to number of flushes during incubation. Nearly half of embryonic deaths that we could age in disturbed nests occurred before hen flushes, and most other losses, including whole clutches, were not clearly caused by investigator disturbance. *Received 30 June 1997, accepted 27 Oct. 1997.*

Information about researcher impact on nesting success is vital in studies of nesting birds (Götmark 1992). Precautions against negative impacts are especially important when studies involve endangered species, such as the Greater Prairie-chicken (*Tympanuchus cupido pinnatus*) in Illinois (Illinois Endangered Species Protection Act of 1972, amended 1977). Some investigations suggest researcher disturbance of nesting prairie-chickens might increase rates of abandonment (Davison 1940, Lehmann 1941, Yeatter 1943, Riley et al. 1992), depredation (Silvy 1968, Bowen 1971, Bowen et al. 1976), or egg breakage (Baker 1953). Other studies, however, report little or no impact with various nest-searching methods (Drobney 1973, Toepfer 1988), including cable-chain drags (Svedarsky 1983, 1988; J. R. Keir, pers. comm.). Search techniques in these studies also included use of dogs, rope drags, flushing bars, landowner interviews, observing departures and returns by nesting hens to morning and evening feeding sites, and most currently, radio telemetry. Thus, reasons for differences in researcher impact on clutch performance are not well known.

Events during two phases of Illinois' 29-year study (1963–1991) of 1101 Greater Prairie-Chicken nests suggested possible researcher-caused bias of egg success. During 1983–1987, egg success was no better in prairie-chicken nests from which parasitic Ring-necked Pheasant (*Phasianus colchicus*) eggs had been removed than for those from which pheasant eggs were not removed (Westemeier 1988). In 1990–1991, during efforts to increase genetic variability by exchanging eggs in two isolated remnant populations, embryonic mortality appeared exceptionally high, though seemingly unattributable to researcher activities (Westemeier et al. 1991). These findings prompted an expanded study.

Our objectives were to determine return rates of Greater Prairie-Chicken hens to their nests after investigator-induced disturbance, compare fates of investigator-disturbed with undisturbed nests, compare embryonic mortality between investigator-disturbed and undisturbed successful nests, and to determine if effects of investigator disturbance varied with stage in nesting cycle, or the number of hen flushes.

METHODS

Study areas and nest searching.—The study areas are located on the southern-till plain of Illinois near Bogota in Jasper County and near Kinmundy in Marion County (Fig.1). Flat-to-rolling prairies between wooded stream corridors characterized the region prior to European settlement. Both areas are now predominantly private farmlands of corn (*Zea mays*), soybeans

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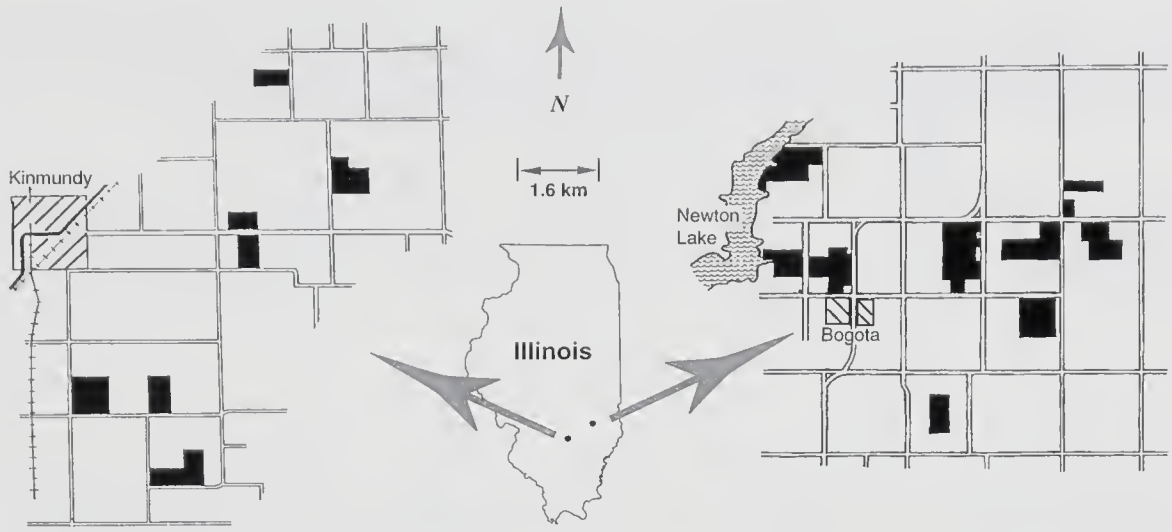

FIG. 1. Study areas near Bogota in Jasper County and near Kinmundy in Marion County, Illinois. Black blocks indicate sanctuary grasslands gradually established and annually managed for Greater Prairie-Chickens and associated wildlife during the study from 1963 through 1991.

(*Glycine max*), and wheat (*Triticum aestivum*). Fifteen scattered tracts (sanctuaries) ranging in size from 7–94 ha and totaling 551 ha (Fig. 1) were established by seeding cropland to grasses during the study (Sanderson et al. 1973; Westemeier 1973, 1988; Westemeier and Buhnerkempe 1983; Buhnerkempe et al. 1984; Westemeier et al. 1991).

During the first 22 years (1963–1984) of research, searching for nests on sanctuary grasslands did not begin until early June. A "hands-off policy" left most study nests undisturbed by researchers until hatching, depredation, abandonment, or other fate had terminated nesting efforts.

From 1985–1991, nest searching commenced by 1 May to allow removal of Ring-necked Pheasant eggs from active (i.e., first egg to termination) Greater Prairie-Chicken nests (Westemeier 1988). Earlier searching resulted in a higher proportion of total nests being found during egg laying or incubation (i.e., disturbed) than in previous years, but the change did not affect the relative stage of nesting (laying or incubating) at which active nests were found during the two periods.

Nest searches involved 2 or more persons walking abreast, each viewing a 1.5-m swath and using a 1.5-m staff to part vegetation at each possible nest site. Fields were searched once each year. We considered nest disturbance to include inspections of active nests even if hens were not flushed, because human scent and tracks were unavoidable. Active nests were marked with blaze orange ribbon placed 10 paces away on two sides of nests forming a right angle with each nest. Markers were tied to vegetation at heights of 30–35 cm. Nests that were already hatched or unsuccessful when found were tagged conspicuously at the immediate nest site for quick relocation and analysis.

Hen flushing.—Our first aim was to determine whether hens, if flushed, returned to their nests during the interval between flushing by investigators and nest termination. When hens were flushed from nests (most inadvertantly), search teams promptly left the sanctuary areas to allow for quick returns. The relatively few instances of intentional flushing for nest inspection were done when no rain was imminent, during midday (11:00–14:00), when temperatures were above 21° C, and at about weekly intervals. Hens were flushed once from 63% of the nests disturbed while active (n = 115) and more than once or not at all from the other 37%. Care was taken to minimize disturbance of vegetation surrounding nests, and attempts were made to restore disturbed plants to their original state.

Nest success.—Nests were considered successful if at least 1 Greater Prairie-Chicken egg hatched, but unsuccessful if only pheasant eggs ($\geq$ 1) hatched in parasitized nests. Vance and Westemeier (1979) reported that parasitized prairie-chicken nests were less successful than unparasitized nests, but later data revealed no difference between unparasitized and parasitized nests (Westemeier 1988). Thus, parasitized nests were included in evaluating nest success.

We estimated nest success using apparent nest success since clutches found after termination (88%) or during incubation (9%) were not aged in this study. Mayfield's nest success (Mayfield 1975) was computed for a small sample (n = 27) of nests found during egg laying, which provided ages of those clutches. We assumed a laying rate of 1 egg/day. Klett and coworkers (1986) considered apparent nest success an appropriate estimator if successful and unsuccessful nests were found with equal probability, a condition that might be met in small units of habitat intensively searched for terminated nests, as in our situation. Nests destroyed by farming activities ($n \geq 92$) and nests of unknown fate (n = 56, $\bar{x}$ = 5.1%/year) were excluded from analyses of nest fate.

Embryonic mortality.—Intact eggs remaining in successful nests were opened and checked for germinal discs or embryos. Embryos were aged by criteria slightly modified from those for Ring-necked Pheasants (Labisky and Opsahl 1958) and Northern Bobwhites (*Colinus virginianus*; Roseberry and Klimstra

TABLE 1. Minimum returns by 107 Greater Prairie-Chicken hens to nests categorized according to flush frequency and stage of nesting when flushed by researchers, south-central Illinois, 1963–1991.

	Nesting stage when flushed							
	Incubating		Laying, incubating[a]		Unknown		Pooled	
Number of times flushed	Hens *n*	Returns[b] %	Hens *n*	Returns %	Hens *n*	Returns %	Hens *n*	Returns %
1	61	95.1	4	75.0	8	12.5	73	84.9
2	15	80.0	5	80.0			20	80.0
3	4	100.0	4	100.0			8	100.0
4	2	100.0	2	87.5			4	93.8
5					2	100.0	2	100.0
1–5	82	91.9	15	88.2	10	61.1	107	87.7

[a] Includes 6 hens flushed a total of 9 times during laying only; 9 hens were flushed during laying and incubation.
[b] Returns after flushing (minimum estimates) verified by subsequent nest success or by observing hens on nests prior to depredation or other fate.

1965). Both species incubate for about 23 days, compared with about 25 days for Greater Prairie-Chickens (Silvy 1968, McEwen et al. 1969, Svedarsky 1988). Rather than considering hatching success of total or fertile eggs, and to avoid bias from infertility or lack of incubation of fertile eggs, we directly evaluated the rate and timing of embryonic losses relative to disturbances. In assessing rates of embryonic mortality, prairie-chicken nests parasitized by pheasants were excluded because of possible bias associated with this interaction; excessive embryonic losses may be attributed to hens leaving their nests prematurely with parasitic broods prior to hatching of Greater Prairie-Chicken eggs (Vance and Westemeier 1979; Westemeier 1984, 1988; Westemeier and Edwards 1987).

Disturbed nests, those in which hens were laying or incubating when found, provided the best estimates of the numbers of total, fertile, and hatched eggs because of their fresh condition. Conversely, in undisturbed nests (eggs hatched, depredated, or abandoned upon discovery), egg shells or contents of intact eggs were often in poor condition by the time of discovery which resulted in minimum estimates of total eggs, fertile eggs, and hatched eggs. Consequently, we selected nests with egg shells and unhatched eggs still sufficiently fresh to detect germinal discs or embryos for calculating embryonic mortality. To verify success, we looked for distinct caps or pointed portions of eggs with detached membranes and pip lines characteristic of hatching. Dates of discovery for successful disturbed nests averaged 25 days earlier than successful undisturbed nests (8 June vs. 3 July, respectively). Thus, we hypothesized that the later dates might have allowed for a disproportionate removal of unhatched eggs by predators in undisturbed nests prior to our inspections. If so, such egg removal might have erroneously indicated less embryonic mortality in undisturbed nests than in disturbed nests.

Statistical analysis.—We used the log-likelihood ratio test (G-test) for contingency tables (Zar 1984) to determine if the frequency of hens returning to their nests (Table 1) was independent of (1) the number of times hens were flushed during incubation (data column one), (2) the number of times hens were flushed during incubation, laying, and unknown stages of nesting (pooled; data column four), and (3) flushing during incubation, or incubation and laying, regardless of the number of flushes (bottom row). Because of the unreliability of asymptotic P values with small sample sizes, we derived exact P values using permutation procedures (Agresti 1990).

We grouped data on nest fate into 3 sets similar to those of Evans and Wolfe (1967) for Ring-necked Pheasants because our methods were similar to theirs. Group I included nests from which hens were flushed at least once; Group II included a few nests found with hens on eggs but never flushed; and Group III included the majority of nests which were undisturbed because hatching, depredation, or other fate had occurred by the time they were found. G-test statistics for contingency tables were used to determine if nest success was independent of (1) flush frequency or (2) stage of nesting, and (3) whether it differed for nests involving hen flushing (Group I) and no disturbance (Group III). We also used G-tests for contingency tables to determine if frequency of nest abandonment or depredation differed between Group I and Group III. The effect of the number of human visits to each nest served as the predictor variable for a separate logistic regression (BMPD 1992) where nest success (score = 1) or failure (score = 0) was used as the dependent variable.

We compared the magnitude of embryonic mortality in disturbed and undisturbed nests using the Normal Approximation to the Mann-Whitney test (Zar 1984). For this test, the nest (% of embryos failing) was the unit of replication since embryos within a nest were not considered independent observations. We used a 1-way Kruskal-Wallis (K-W) test (BMPD 1992) to assess the association between the number of hen flushes and % embryonic mortality by grouping nests (1 flush, 2 flushes, ≥3 flushes).

RESULTS

Hen returns after flushing.—Of 1101 Greater Prairie-chicken nests found in south-

central Illinois during 1963–1991, 115 were active (egg laying, n = 27; incubation, n = 78; unknown n = 10) upon discovery. Eight active nests had no hen flush; the other 107 hens flushed 1–5 times [$\bar{x}$ = 1.5 ± 0.9 (SD) flushes/hen]. After 163 flushes among 107 hens, we documented at least 143 returns (minimum rate = 88%) by hens to their nests prior to hatching, depredation, or abandonment. Small samples involving hens flushed 3–5 times appeared to show higher return rates than larger samples with hens flushed 1–2 times (Table 1). Statistically, however, the return rate decreased with increased frequency of hen flushing during incubation (G = 12.63, df = 3, P < 0.01) [e.g., we could not be certain that 6 of 15 incubating hens returned after two flushes (Table 1) because of depredation or abandonment after the second flush]. Similarly, minimum hen returns also showed a tendency to decline (G = 9.76, df= 4, P = 0.042) with increased frequency of flushing during incubation, laying, or unknown stages of nesting (pooled; Table 1). Again, we could not be certain that some hens returned, particularly after two flushes. Proportions of hens returning to nests during incubation, or both laying and incubation (two independent groups) did not differ (G_c = 1.32, df = 1, P > 0.05) regardless of flush frequency (Table 1).

Nest success after hen flushing.—Nest success did not differ whether hens were flushed 1, 2, or at least 3 times (G = 2.90, df= 2, P > 0.05); thus, nests experiencing at least 1 flush constituted Group 1 (Table 2). Within Group 1, there was no difference in nest success between hens flushed during incubation and those flushed during laying (G_c = 1.58, df = 1, P > 0.05). Sample sizes in Group II were too small for tests. Success was actually higher (G_c = 7.55, df = 1, P < 0.01) for Group I (hens flushed by investigators) than for Group III (hens not flushed because hatching or other fate occurred prior to nest discovery). No relationship was shown between nest success and the number of times active nests (Groups 1 and II combined) were visited ($F_{1,111}$ = 0.46, P > 0.05). Successful, abandoned, and depredated nests were visited an average of 1.9, 2.0, and 2.1 times, respectively, prior to termination. Nest success calculated by the Mayfield exposure method was 59% for 27 nests found during the laying stage.

Abandonment and predation after hen flushing.—Frequency of abandonment was no higher for nests with hen flushes (Group I) than for undisturbed nests (Group III; G_c = 0.03, df = 1, P > 0.05; Table 2). Predation was less for nests from which hens were flushed (Group I) than for undisturbed nests (Group III; G_c = 9.04, df = 1, P < 0.005). In the few active nests where hens were not flushed (Group II), no abandonment was observed and depredation was 38%.

Embryonic mortality after hen flushing.—Of the 4,591 embryos in 479 successful Greater Prairie-Chicken nests from several counties in southcentral Illinois during the 29-year study, the rate of embryonic deaths

TABLE 2. Fate of 953 Greater Prairie-Chicken nests categorized according to degree of disturbance by nest searchers and stage of nesting, south-central Illinois, 1963–1991.

			Nest fate[a]					
			Successful		Abandoned		Depredated	
Category	Nesting stage when found	n	n	%	n	%	n	%
Group I (Hen flushed)	Incubating	81[b]	63	77.8	5	6.2	13	16.1
	Laying	14	8	57.1	1	7.1	5	35.7
	Unknown	10	0	0.0	0	0.0	10	100.0
	Total	105	71	67.6	6	5.7	28	26.7
Group II (Hen on, no flush)	Incubating	4	3	75.0	0	0.0	1	25.0
	Laying	4	2	50.0	0	0.0	2	50.0
	Total	8	5	62.5	0	0.0	3	37.5
Group III (No hen, undisturbed)	Hatched or unsuccessful							
	Total	840	446	53.1	40	4.8	354	42.1

[a] Omits nests of unknown fate and those destroyed by farming.
[b] Includes 7 nests found in laying stage with no hen present, but hens were later flushed during incubation.

(% in each nest) was 3.7× higher in disturbed nests [n = 56, $\bar{x}$ = 12.2 ± 2.2 (SE)], than in undisturbed nests (n = 423, $\bar{x}$ = 3.3 ± 0.4; Z = 4.59, P = 0.001). Embryonic mortality was unrelated to the number of flushes (1, 2, or ≥ 3) during incubation of successful unparasitized nests (K-W test: H = 0.38, df = 2, P > 0.05).

Clutch size was determined during incubation for 74 disturbed successful nests. These provided insight to possible bias in embryonic mortality resulting from egg predation during the 25-day average difference in discovery dates for disturbed and undisturbed nests. At our final post-hatch inspections, 1–3 intact eggs, or egg shells were missing in only 7 of the 74 nests of known clutch size. One egg disappeared between two inspections during incubation. Losses occurred in six other nests either during incubation or within 6 days after hatching. No losses of whole eggs or egg shells occurred in 67 nests; this included 16 nests that contained intact eggs when examined 7–14 days after hatching of other eggs.

Knowledge of hatch dates, inspection dates, and embryo age at death was sufficient in most disturbed nests with embryo losses to assess the timing of mortality relative to timing of hen flushes. Thus, 47% of the losses occurred prior to hen flushes, 20% coincided with hen flushing, 23% occurred well after hen flushes, and 10% occurred at an indeterminate time. Losses clearly resulting from nest searching included three eggs stepped on and one egg punctured, presumably by a hen's toenail when she flushed.

DISCUSSION

During this 29-year study, at least 88% of Greater Prairie-Chicken hens readily returned to their nests after 1–5 flushes. The calculated proportion of hens returning might have been considerably higher had we been able to verify some returns prior to depredations. As expected, disturbed nests, most of which were well along in incubation when found, were more successful than undisturbed nests already hatched or unsuccessful upon their discovery. Clutches found within a few days of hatching are more likely to hatch than those in the laying or early incubation stages because of the shorter interval between discovery and hatching (Mayfield 1975, Klett et al. 1986). This may partly account for the greater success of disturbed nests (68%) than undisturbed nests (53%). The 59% rate for Mayfield nest success also was relatively high (Jones 1988, McKee 1995) for 27 nests found during laying.

In our study, the probability of finding depredated prairie-chicken nests may have been at least equal to finding active nests. Incubating hens are often reluctant to flush (and be found), but bright, exposed, and often-scattered egg shells in depredated nests contrast with grassy vegetation. For these reasons, any bias may have favored our finding a greater proportion of unsuccessful nests rather than active and potentially more successful nests. This contention differs from that of Johnson (1994) for ducks. Thus, the relatively high success of disturbed prairie-chicken nests (68%) may have been even higher, not lower, than that for undisturbed nests that were no longer active when found.

For pheasant nests visited during incubation, Evans and Wolfe (1967) showed that rates of success and abandonment were not different from those of hens with which the investigator had no contact. Success for 934 prairie-chicken nests in 22 previous studies averaged 49% (Bergerud and Gratson 1988), which is similar to success of undisturbed nests in our study.

In our study, abandonment of 6 nests disturbed by researchers involved infertile eggs, possible pheasant interactions, or photographer disturbance (1 nest that also involved a non-researcher using a blind); none were clearly caused by investigator disturbance. Desertion of Prairie-Chicken nests (n = 876) averaged 7.3% in 18 previous studies (Bergerud and Gratson 1988). Other studies suggest that desertion may be increased if disturbance occurs during early stages of nesting for Greater Prairie-Chicken (Yeatter 1943), Blue Grouse (*Dendragapus obscurus*; Zwickel and Carveth 1978), and other species (Götmark 1992). Our limited observations indicated tolerance by hens flushed from eggs once the hens are at least midway through laying.

Nest predation following hen flushing was relatively low in this study (27%), possibly because of the short interval remaining before hatching in advanced clutches (Klett et al. 1986). Predation on 934 prairie-chicken nests

in 22 previous studies averaged 39% (Bergerud and Gratson 1988), which is similar to predation on undisturbed nests (42%) in our study. When active nests were initially found by a crew of nest searchers, tracks and human scent were uniformly distributed over the searched portions of fields, and 63% of 115 nests were visited only once. Thus, there were no direct trails, which are commonly thought to lead predators to nests, to nearly two-thirds of the disturbed nests. In an extensive review, Götmark (1992) found no or little evidence for increased predation by mammals on bird nests as a result of investigator disturbance. In Kansas, Bowen et al. (1976) found no difference in depredation rates on dummy nests walked to daily compared with unvisited control nests. However, normal feeding patterns of Greater Prairie-Chickens tending real nests were disrupted in an earlier study (Bowen 1971). Flushing incubating prairie-chickens from their nests during midday (as in our study) is likely to be additive to their normal absence for feeding during early morning and late afternoon (Silvy 1968, Bowen 1971, Svedarsky 1979).

For average clutches of 11.2 fertile eggs, a 12.2% embryonic mortality rate means 1.4 dead embryos per disturbed active nest if losses prior to hen flushes (nearly half in our study) are included, compared with a normal loss of 0.4 embryo per undisturbed clutch. Other studies indicate embryonic mortality (unsuccessful fertile eggs/total fertile eggs) well below 10% (Gross 1930, Hamerstrom 1939, Yeatter 1943, Svedarsky 1988, Jones 1988), and even no loss (Schwartz 1945, Baker 1953, Silvy 1968, Drobney 1973). However, removal of unhatched eggs by predators prior to post-hatch inspections may have biased data from other studies, as in our study.

By 7 days post hatch, sterile eggs or those with dead embryos may be sufficiently putrid to be unappealing to predators. Our experience suggests that partial disappearance of eggs or egg shells mostly occurs between late incubation and 1 week post hatch. Since we typically delayed final nest inspections to about 4 days post hatch, bias associated with nest discovery dates seems minimal because much of the time frame for egg loss may have applied to disturbed and undisturbed nests alike. Yet, despite precautions taken to minimize negative effects to disturbed clutches in Illinois, embryonic mortality appeared excessive. Some hens may be slow in returning to their clutches after being flushed, and the eggs may subsequently experience excess exposure to sun, cooling, or drying with attendent weakening and killing of embryos.

We conclude that our nest study methods have allowed a minimum of 88% return of disturbed hens to their nests and nest success at least as good as their undisturbed counterparts. However, embryonic mortality in disturbed nests appeared high even with considerations for bias. The causes of embryonic mortality remain largely enigmatic and perhaps exclusive to Illinois. A loss of egg quality possibly stemming from genetic deficiencies should not be ignored because Greater Prairie-Chicken populations in Illinois are small, isolated, and had declined alarmingly during the period (1987–1991) of highest embryonic loss (Westemeier et al. 1991). In future studies, flushing of nesting hens should be minimal, but when flushing is necessary, the time of day, date, weather conditions, and egg exposure should be routinely recorded for evaluations of embryonic mortality. Improved knowledge of laying times and daily off-nest feeding periods by incubating hens would facilitate nest inspection and obviate hen flushing. An aging guide for Greater Prairie-Chicken embryos is needed. Controlled experiments on the effects of various stresses on survival of Greater Prairie-Chicken embryos and pen studies on interactions with pheasants might provide needed information.

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FACTORS AFFECTING THE SIZE OF FERRUGINOUS HAWK HOME RANGES

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ABSTRACT.—We used radio-telemetry to track movements of seven adult male Ferruginous Hawks (*Buteo regalis*) in southcentral Washington. Home range size was estimated for each male using minimum convex polygon, harmonic mean, adaptive kernel, and fixed kernel-based methods. Minimum convex polygon and harmonic mean home ranges were significantly larger than those previously reported for Ferruginous Hawks. Home ranges varied substantially among males (mean = 90.3 km^2, range = 17.7–136.4 km^2). There was no relationship between home range size and brood size; however, there was a significant relationship (r^2 = 0.964, P = 0.018) between home range size and the distance from the nest site to the nearest irrigated agricultural field where some males hunted. Kernel-based estimates showed two distinct core areas for most males, one around the nest and a second in the agricultural fields where they hunted. *Received 25 Aug. 1997, accepted 29 Oct. 1997.*

The Ferruginous Hawk (*Buteo regalis*) is a large grassland raptor that breeds in the shrub-steppe and semi-arid regions of western North America (Olendorff 1993). The species is thought to be sensitive to human-caused disturbance in its nesting areas (Lokemoen and Duebbert 1976, Bechard et al. 1990). Habitat degradation caused by agriculture and overgrazing have been reported as a threat to the species' survival in North America (Howard 1975, Thurow et al. 1980, Cottrell 1981, Gilmer and Stewart 1983). In Oregon and Washington, the species is on the periphery of its range and is currently listed as Threatened in Washington which has an estimated population of 50 to 60 breeding pairs (Wash. Dept. Fish Wildl. 1996). This study was undertaken to provide information about the spatial use patterns of the Ferruginous Hawk in southcentral Washington for use by the state Department of Fish and Wildlife in their recovery plan for the species.

Herein, we report home range estimates for adult male Ferruginous Hawks in southcentral Washington and compare them with results previously reported in the literature. We estimate home range size using four different techniques: the minimum convex polygon (MCP; Mohr 1947), harmonic mean (Dixon and Chapman 1980), fixed kernel, and adaptive kernel-based (Worton 1989, Kenward 1990) methods. Lastly, we relate variability in individual home ranges to factors such as brood size and habitat type around the nest site, and examine possible effects of habitat on home range size.

STUDY AREA AND METHODS

We conducted the study on and adjacent to the 1482 km^2 U.S. Department of Energy's (DOE) Hanford Site (site) located in Benton and Franklin counties, Washington. The Columbia River borders the site to the north and east and the Yakima River borders the site to the south. Rattlesnake Mountain, at 1100 m above mean sea level on the western boundary, is the main topographic feature in the region. With the exception of Rattlesnake Mountain and the Horse Heaven Hills south of the site, topography is relatively flat.

The study area is in the sagebrush (*Artemesia tridentata*)/bluebunch wheatgrass (*Agropyron spicatum*) vegetation zone described by Daubenmire (1970). Climate is hot and dry during summer and moderately cold and wet during winter. Annual precipitation averages 16.5 cm, but ranges from 7 to 30 cm.

There has been no grazing or agricultural production on the Hanford Site for the past 50 years. However, the site is dominated by a recovering sagebrush/cheatgrass (*Bromus tectorum*) vegetation type characteristic of areas that have recently burned. Areas surrounding the Hanford Site in Benton and Franklin counties are intensively managed for agriculture. South and west of the site, dryland farming (e.g., dryland wheat production) is the primary land use. East of the site and along the Yakima River to the south, the land is used to

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produce crops that require irrigation (e.g., alfalfa and potatoes).

We searched for occupied nests during nest building and incubation periods (March through early May) of 1994 and 1995. Surveys were conducted by scanning from a vehicle or on foot using 10× binoculars and a 60× spotting scope. Initial surveys targeted historical nest locations and were conducted from a distance of more than 100 m to minimize the risk of researcher-caused abandonment. Surveys were also conducted in other areas of suitable habitat (Bechard and Schmutz 1995) to locate new territories. Once located, occupied nests were monitored at least three times each week from a distance more than 100 m for the remainder of the incubation period to determine approximate hatching dates.

We trapped adult Ferruginous Hawks during the early brood rearing portion of the nestling season (when young were about 10 days old), which occurred between 17 May and 3 June 1994 and between 16 May and 10 June 1995. We used a dho-gaza net placed near the nest with a live Great Horned Owl (*Bubo virginianus*) for a lure (Bloom 1987). Six adult males were captured in 1994 and three in 1995. Each male was fitted with a 15-g Advanced Telemetry Systems (Isanti, MN) radio-transmitter, which was tied and glued to the two newest looking retrices, and a U.S. National Biological Service aluminum leg band was attached to the right leg. We measured the toe pad length, mass, and wing chord of each individual captured to verify sex (Gossett 1993).

Tracking began the day after capture and continued until the male could no longer be located in his home range (approximately mid-July). All locations were based on visual observations of perched or flying hawks and locations were obtained during all daylight hours. During the course of the breeding season, we attempted to locate each male at least five times during each of nine different two-hour periods [e.g., 04:00–05:59, 06:00–07:59, etc. (PST)], in order to include observations during all possible activity periods. We attempted to locate each male at least one time every other day. Once located, the male was observed for as long as possible. However, because of large home ranges that often crossed the Columbia River, extended observations were often not possible.

When we began a second study of dietary habits (Leary 1996), one male was tracked continuously for 4–5 h each day. However, a minimum of a 1-h interval was maintained between successive recorded locations to avoid auto-correlation (Andersen and Rongstad 1989). Although probably not statistically independent (Swihart and Slade 1985), we considered locations taken at 1-h intervals to be biologically independent (Lair 1987, Ganey and Balda 1989). In support of this assumption, we observed that a male could easily travel over its entire home range within 1 h. All locations were recorded where the hawk was observed with a Magellan Geographical Positioning System (GPS) using Universal Transverse Mercator (UTM) coordinates. Locations taken with this GPS unit are accurate to ± 100 m, so we consider home range estimates to be accurate to 0.1 km^2. While tracking males and doing nest observations for our study of dietary habits; the time, location, habitat, and outcome of all foraging strikes observed were recorded.

Home range size was estimated for each male based on the 95% MCP (Mohr 1947), kernel (Worton 1989), and harmonic mean (Dixon and Chapman 1980) methods. All estimates were calculated using Ranges V software (version 5.1; Kenward 1990) on an IBM-compatible computer. We estimated home ranges using the 95% MCP method because it is the one most commonly reported in the literature. Because of small sample sizes and unequal variances among results from this and previous studies, we used a nonparametric Mann-Whitney test (Zar 1984, SAS Institute 1990) to compare our results with those reported previously for Ferruginous Hawks.

We used the 95% MCP method to calculate area observation curves for each male and to determine whether sample sizes were large enough to give accurate estimates of home range size (Odum and Kuenzler 1955). To test this, we randomly selected five locations for each individual and estimated the 95% MCP home range. The process was repeated, randomly adding five more locations and estimating home range size until all locations had been included. At the point where each additional location produced less than a 1% increase in the home range size, sampling was deemed adequate.

Linear regression (Zar 1984) was used to determine if home range size was related to brood size or if home range size was related to the distance from nest to the nearest irrigated agricultural fields. For all statistical tests, probability values of ≤ 0.05 were considered significant.

Using the harmonic mean and kernel-based methods, we estimated home range size using nine contour levels to determine which one most accurately described the area used by each male. With the adaptive kernel method, we also estimated home ranges for each male using eight smoothing factors (Worton 1989, Kenward 1990).

RESULTS

We estimated home range size for seven of nine males that were radio-tracked during 1994 and 1995 (Table 1). One male removed its transmitter less than one week after attachment so home range data were not available for that individual. Another male (Webber Canyon) was excluded from the analysis because he did not breed (he was a floater). The Route 2 male was captured and tracked both in 1994 and 1995 when it used the same nest. For analysis purposes, we considered data collected on this male during the two years as separate and independent estimates.

An average of 60 locations (range 16–110)

TABLE 1. Minimum convex polygon home range estimates for seven adult male Ferruginous Hawks in southcentral Washington during 1994 and 1995. Sample size is number of locations taken.

Bird	95% MCP home range[a]	Sample size	Days tracked
Beck Road (1994)	122.7	52	39
Chandler Butte (1994)	75.0	60	54
FFTF #1 (1994)[b]	8.9	40	32
Rt. 2 (1994)	100.5	88	61
Rt. 2 (1995)	89.3	51	42
WPPSS #1 (1995)	136.4	110	58
FFTF #4 (1995)	17.7	16	9[c]
Mean	78.6	60	42

[a] Home ranges in km^2.
[b] Not included in any analysis.
[c] Transmitter failed after 9 days.

were obtained for each male (Table 1). Based on area observation curves (Odum and Kuenzler 1955), adequate sampling was achieved for all but one male (FFTF #1). Therefore, data from this male were not included in the analysis.

With the exception of FFTF #1, all males spent much of their time long distances from their nests. Three males were located more than 10 km from their nest 27% of the time (Fig. 1). As a result, home ranges covered extensive areas. Mean home range size calculated using the 95% MCP method was 90.3 km^2 (SD = 41.9, range = 17.7–136.4 km^2, n = 6; Table 1). We compared these results with those reported by Platt (1984), McAnnis (1990), and Harmata (1991) using a Mann-Whitney test; home ranges from our study (Fig. 2) were significantly larger (P = 0.001). Results from Smith and Murphy (1973), Wakeley (1978), and Janes (1985) were excluded from statistical comparisons because they did not use radio-telemetry to determine home range size. Mean home range size from our study was approximately 17 times that predicted for a raptor on the basis of body mass (Newton 1979).

Variability in home range size among males was not related to brood size (r^2 = 0.238, P > 0.05). In fact, the WPPSS #1 male fledged one young and had a home range of 136.4 km^2, while the FFTF #4, Chandler Butte, and Beck Road males fledged three young each and had home ranges of only 17.7, 75.0, and 122.7 km^2, respectively.

Home range size was significantly related to distance from the nest to the nearest irri-

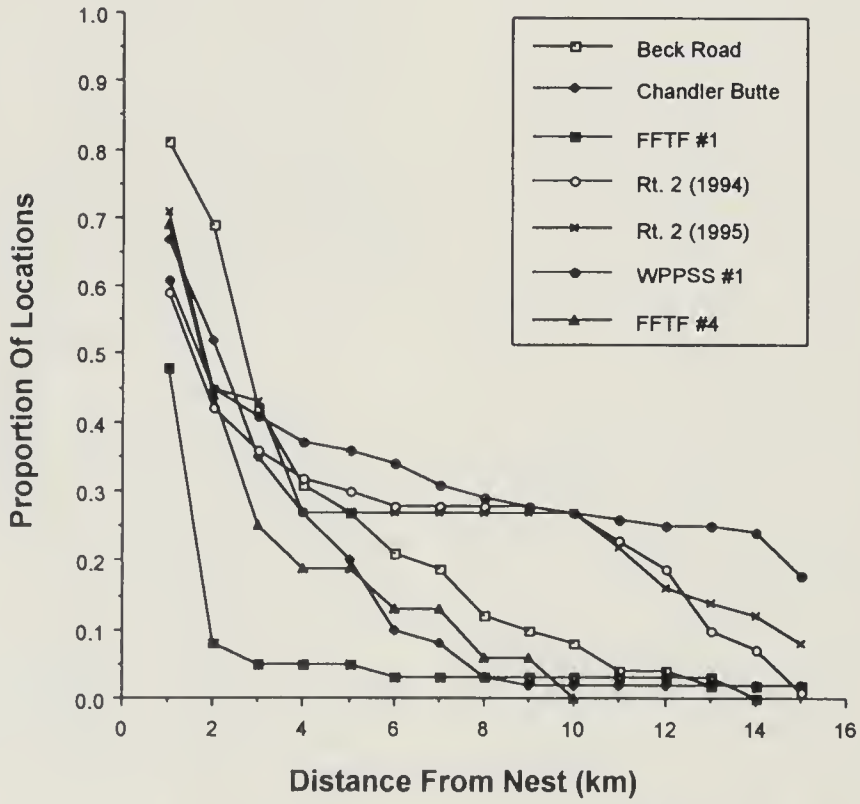

FIG. 1. Distance from the nest site for telemetry locations of seven adult male Ferruginous Hawks in southcentral Washington during 1994 and 1995. Symbols represent the proportion of locations that were greater than that distance from the nest site.

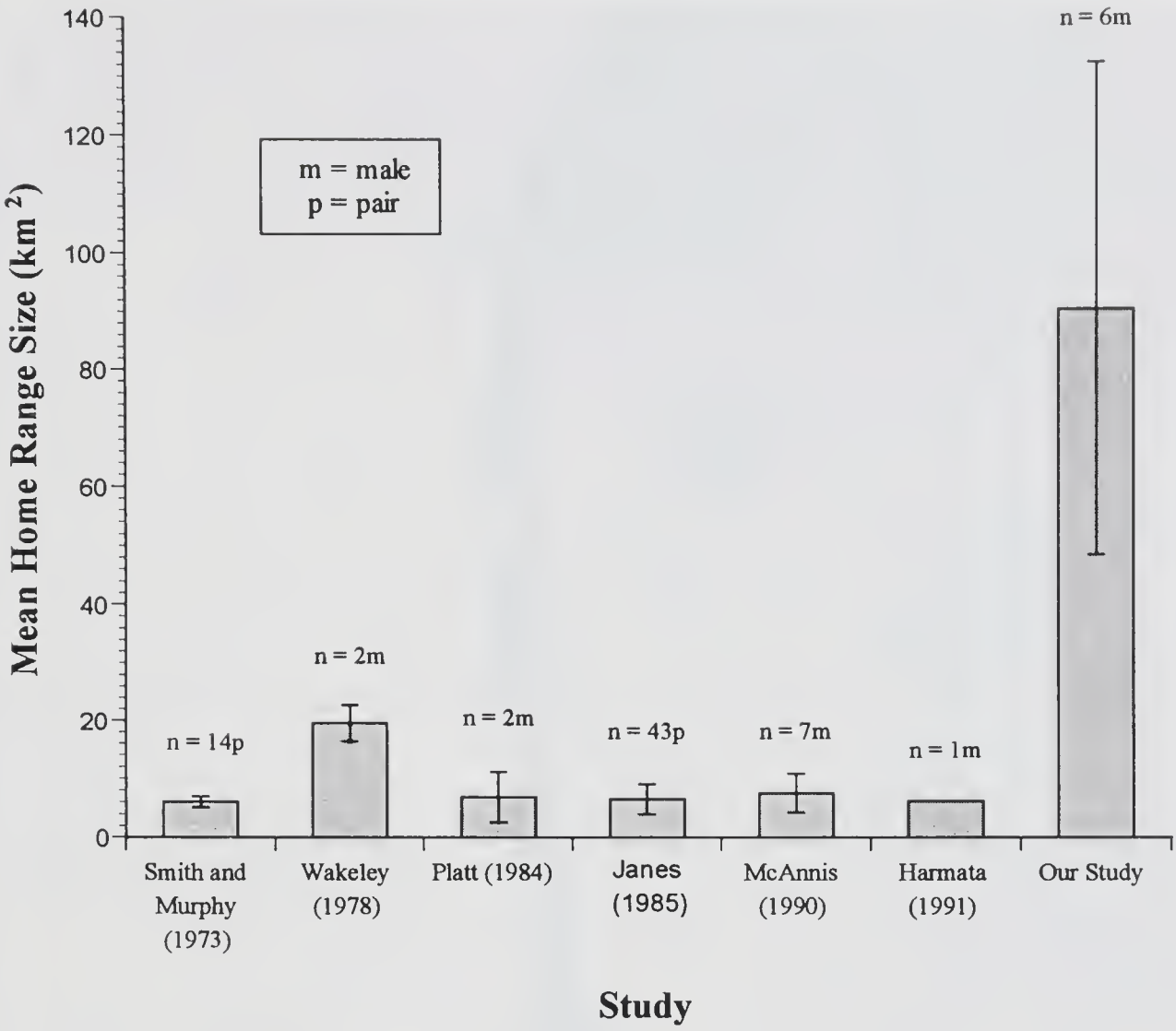

FIG. 2. Comparison of 95% minimum convex polygon mean home range estimates from this study with those previously reported in the literature for Ferruginous Hawks.

gated agricultural field, for the four males that foraged extensively in those fields ($r^2 = 0.964$, $P = 0.018$). FFTF #4 nested closest to the surrounding agricultural fields (1100 m) and had the smallest home range (17.7 km^2), while WPPSS #1 nested the farthest from agriculture (7000 m), and had the largest home range (136.4 km^2).

Despite being successful on 21% of the foraging strikes that occurred in shrubsteppe habitats compared to only 14% of strikes in agricultural fields, all but one male (FFTF #1) hunted extensively in agricultural fields. Of the 49 foraging strikes observed, 71% occurred in agricultural fields. This result may underestimate the importance of agricultural fields because of difficulty in following individuals and observing strikes in fields more than 10 km from the nest. In comparison, strikes that occurred in shrubsteppe habitats were usually within 400–500 m of the nest site and therefore were easily observed. Adults were occasionally observed hopping on the ground late in the evening near their nests, apparently eating insects. However, because we were not certain that they were foraging, these observations were not counted as foraging strikes.

Four males that nested on the site hunted primarily in distant agricultural fields, producing two activity centers or core areas within their home ranges (Fig. 3). One core area was centered in the shrubsteppe habitat around the nest and the second was far removed in the agricultural fields where the individual was hunting. Portions of the ranges between these two core areas were used only as travel corridors. There was a wide variation in core area estimates using different methods, different contours, and different smoothing parameters

FIG. 3. Locations and home range estimates (95% MCP and 85% adaptive kernel with 0.7 smoothing parameter) for the WPPSS #1 male. This home range, with its two core areas, is representative of the home ranges of all males who nested on the Hanford Site and hunted in the agricultural fields that surround the site.

(Table 2). Based on the clustering of fixes, we suggest that the 85% adaptive kernel method with a smoothing parameter of 0.7 best represented the area actually used by each male (Fig. 3). Using this method, mean core area size was 35.0 km^2 (SD = 18.3, range = 7.7–60.3, n = 6). No previous reports of Ferruginous Hawk home ranges have used this method for estimating core areas. However, McAnnis (1990) used the 50% harmonic mean method to estimate core areas for Ferruginous Hawks in southern Idaho and obtained a mean core area of 2.2 km^2. Using the 50% harmonic mean method, mean core area

TABLE 2. Comparison of core area estimates for seven adult male Ferruginous Hawks using three different non-parametric estimation techniques (all estimates in km²). Also shown are estimates from the adaptive kernel-based method using two different smoothing parameters (1.0 and 0.7).

Bird	85% Harmonic mean	85% Fixed kernel	85% Adaptive kernel (1.0)	85% Adaptive kernel (0.7)
Beck Road	73.4	80.3	64.1	45.1
Chandler Butte	73.2	63.5	35.7	22.1
FFTF #1	9.7	7.7	6.8	5.7
Rt. 2 (1994)	71.0	66.5	61.4	38.7
Rt. 2 (1995)	94.3	104.9	49.2	35.8
WPPSS #1	89.8	88.5	75.1	60.3
FFTF #4	17.2	35.0	11.3	7.7
Mean	61.2	63.8	43.4	30.8

from our study was 8.7 km², which is significantly larger than the core areas reported by McAnnis (1990; $P = 0.005$).

DISCUSSION

Using the MCP method, home ranges from our study were significantly larger than those reported in previous studies on Ferruginous Hawks (Smith and Murphy 1973, Wakeley 1978, Platt 1984, Janes 1985, McAnnis 1990, Harmata 1991). Differences in home range estimates among studies may reflect differences in habitat quality or prey densities. Newton (1979) demonstrated a relationship between home range size and habitat quality, which translates to prey density and prey vulnerability, for the European Sparrowhawk (*Accipiter nisus*). A similar relationship may also exist for Ferruginous Hawks.

Habitat quality or prey availability at our site may have been poorer than at other studied sites. For example, McAnnis (1990) reported the majority of foraging attempts in her study area occurred within 1 km of the nest site. In our study area, males consistently traveled distances greater than 10 km from the nest site to forage in irrigated agricultural fields. Kernel analysis revealed two distinct core use areas where the male either roosted or hunted. The distance between these core areas was closely related to the distance from the nest to irrigated agricultural fields. This suggests that prey may have been less available in habitats around nest sites and more available in the irrigated agricultural fields.

Wakeley (1978) did not report estimates of core areas, but he did indicate that a high proportion of locations were in a small portion of the home range and that both males in his study used one block of their range for the majority of their foraging activities. His home range diagrams include large areas that were never used by the hawks. McAnnis (1990) reported core areas using the 50% harmonic mean method. Core areas in her study were concentrated around the nest site, indicating that males were foraging and resting in the same areas. Because of the way in which locations were distributed in our study, the harmonic mean method also included large areas that were never used by the male.

The home ranges of the hawks we observed were large and often crossed rivers and other geographical features; therefore, visual observations would not have been possible without the use of radio-telemetry. We rarely observed males foraging within sight of their nests. In fact, three of the males were observed foraging more than 15 km from their nest. In contrast, Smith and Murphy (1973), Wakeley (1978), and Janes (1985) observed birds and estimated home ranges without the use of telemetry, indicating that males in their studies did not travel far from the nest site during any of their daily activities.

Wakeley (1978) indicated that males do all of the hunting for the family during incubation and most of the brood-rearing season. He did not observe females hunting until young were almost one week from fledging. Although we did not use radio-telemetry to track females, on several occasions while tracking males and conducting nest observations (Leary 1996), we observed females out hunting when their young were only two weeks old. This behavior may be another indication that food was less available. Males may have been unable to provide for the entire family because of the long distances they had to travel to find prey.

Wakeley (1978) reported that alfalfa fields were the only places where he found appreciable numbers of northern pocket gophers (*Thomomys talpoides*), the primary prey species of Ferruginous Hawks in his study area. Schmutz (1987) determined that ground squirrels (*Spermophilus* spp.), another favorite prey species of the Ferruginous Hawk, also occurred in high numbers in agricultural fields.

Bechard (1982) found that prey was most abundant in cultivated fields, but that Swainson's Hawks (*Buteo swainsoni*) did not hunt in these fields until crop harvest reduced the density of the plant canopy. We observed male Ferruginous Hawks hunting in alfalfa fields throughout the breeding season. This may have been possible because alfalfa fields are typically harvested several times a year enabling hawks to consistently find fields with low canopy cover.

All nests on the Hanford Site were located in a recovering (recently burned) sagebrush/cheatgrass habitat. Nests off the site were surrounded by dryland agriculture (primarily wheat fields), but off-site males also had large home ranges. This may have been related to the fact that wheat fields are only harvested once a year near the end of summer and thus have high canopy cover throughout most of the breeding season. This probably limited prey availability, forcing males nesting and foraging in dryland agricultural areas to travel long distances to locate prey. Wakeley (1978) determined that canopy cover was the most important factor influencing choice of foraging habitats for Ferruginous Hawks, and these hawks used dense cover habitats such as grass, rush grass (primarily *Juncus* spp.), and grain fields significantly less than expected based on availability. Bechard (1982) also found canopy cover to be an important factor in the choice of foraging areas for Swainson's Hawks.

Several authors have reported that the conversion of native habitats to agriculture and other uses may threaten the Ferruginous Hawk (Howard 1975, Thurow et al. 1980, Cottrell 1981, Gilmer and Stewart 1983, Schmutz 1984). Others have reported negative impacts of agriculture on breeding densities and productivity of the species (Schmutz 1989, Olendorff 1993). Howard and Wolfe (1976) predicted that the conversion of native vegetation to monotypic stands of agricultural crops might reduce breeding densities and reproductive success because of increased disturbance, loss of nest sites, and the reduction of prey populations. To the contrary, our data indicate that in areas where prey densities are low, Ferruginous Hawks rely on agricultural fields for foraging. Our findings that Ferruginous Hawks traveled out of shrub-grassland habitats and into agricultural areas suggest that some types of agriculture, such as alfalfa fields, can be beneficial to these hawks.

Ferruginous Hawks in our study area may nest on the Hanford Site and forage in distant agricultural fields because of a lack of suitable nest sites in the agricultural areas or because there is too much disturbance in those areas. To further our understanding of this species' ecology, future research should examine prey densities in the various habitats and assess female activity budgets. Olendorff (1993) suggests constructing artificial nest platforms for Ferruginous Hawks in areas of suitable habitat. This should be considered as a management strategy in our study area.

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DISPERSAL MOVEMENTS AND SURVIVAL RATES OF JUVENILE MEXICAN SPOTTED OWLS IN NORTHERN ARIZONA

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BRENDA E. STROHMEYER,[1] AND JEFFREY S. JENNESS[1]

ABSTRACT.—We monitored dispersal movements of 19 radiotagged juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in northern Arizona during 1994 and 1995. All juveniles initiated dispersal movements in September or October during both years, with most dispersing during September. Initial dispersal movements were rapid and abrupt, but lacked a significant directional pattern. Distance from the nest to the last observed location and the most distant location reached ranged from 0.6–72.1 and 2.1–73.5 km for individual owls, respectively. These distances represent minimum estimates of dispersal capability because only one individual was tracked until it settled on a territory and paired. Owls used a variety of habitat types during dispersal, some of which differed markedly from typical nesting habitat for Mexican Spotted Owls. Four of five owls that were tracked past mid-November moved to lower elevation pinyon-juniper woodlands and at least one overwintered in pinyon-juniper woodland. Kaplan-Meier estimates of annual survival rate ranged from 20.5–28.7%, depending on whether we censored all owls with unknown fates or included suspected deaths as mortality events. Estimates differed significantly between years and confidence intervals were wide, suggesting that longer-term studies of large numbers of owls will be required to obtain accurate and precise estimates of juvenile survival. *Received 8 May 1997, accepted 21 Jan. 1998.*

Mexican Spotted Owls (*Strix occidentalis lucida*) are widely but patchily distributed throughout the southwestern United States and northern Mexico (Ward et al. 1995), apparently reflecting the disjunct distribution of the forested mountains and canyonlands they occupy (Ganey and Dick 1995). This subspecies was listed as Threatened in 1993, primarily because of concerns over the effects of loss of forested habitat on the owl (Block et al. 1995).

Recent planning efforts have demonstrated the importance of accurate estimates of juvenile survival and knowledge of dispersal patterns to understanding population processes in the Spotted Owl (Thomas et al. 1990, Noon and McKelvey 1992, Keitt et al. 1995, White et al. 1995, Forsman et al. 1996). Despite these findings, few data exist on either dispersal movements or juvenile survival rates for the Mexican Spotted Owl. Keitt and coworkers (1995: fig.1) summarized unpublished data on dispersal of Mexican Spotted Owls from two study areas (Gutiérrez et al. 1994). However, estimates of dispersal distance were based on resightings of color-banded birds on a study area of limited size. This methodology likely underestimates both dispersal distance and juvenile survival because birds that move long distances have a greater probability of leaving the study area and never being resighted (White et al. 1995, Burnham et al. 1996). The only other information on dispersal of juvenile Mexican Spotted Owls is in unpublished reports (Willey 1995, Hodgson and Stacey 1996). These studies indicated that radiotagged juveniles initiated dispersal from August–October, moved rapidly and over long distances, and sometimes crossed open habitats very different in structure from typical nesting habitat. Similar patterns were reported with respect to dispersal movements of both Northern (*S. o. caurina*) and California (*S. o. occidentalis*) Spotted Owls (Forsman et al. 1984, Gutiérrez et al. 1985, Laymon 1988, Miller 1989, Miller et al. 1997).

Estimates of annual survival rates of juvenile owls exist for all three subspecies of Spotted Owls (Noon et al. 1992: table 8G, White et al. 1995: table 2.2, Burnham et al. 1996: table 4). All of these estimates were based on mark-recapture studies and may be biased if emigration from the study area is common. Only Burnham and coworkers (1996) adjusted their estimate for emigration of marked owls from the study areas; their adjustment was based on data on the movements of radiotagged juveniles.

To provide better information on dispersal of juvenile Mexican Spotted Owls, we studied

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dispersal movements and survival of radiotagged juveniles. Our objectives were to (1) monitor movements of dispersing Spotted Owls, to document timing of dispersal, movement rates and patterns, and habitat use; and (2) estimate first-year survival rates of Mexican Spotted Owls based on observations of radiotagged juveniles.

METHODS

Study areas.—We captured and radiotagged juvenile owls in three discrete areas in northcentral Arizona. These areas were located on the (1) Mormon Lake and Long Valley Ranger Districts, Coconino National Forest; (2) Chevelon Ranger District, Apache-Sitgreaves National Forest; and (3) Williams Ranger District, Kaibab National Forest. Elevation ranged from approximately 1800–2660 m within all three study areas, and the climate in all three areas featured cold winters and warm summers.

The Coconino study area was located approximately 40 km south of Flagstaff in northcentral Arizona. Topography of this area was relatively flat with scattered cinder cones and volcanic mountains. The area consisted primarily (73%) of ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelli*) forest, intermixed with mixed-conifer forest (14%) dominated by Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*), ponderosa pine forest (10%), pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) woodland (2.7%), and grasslands (0.7%; percentages from Gutiérrez et al. 1994).

The Chevelon study area was located approximately 60 km south of Winslow, Arizona. This area was dominated by a series of major drainages running north from the Mogollon Rim, a prominent geologic uplift, to the Little Colorado River. Vegetation in the area consisted primarily of mixed-conifer forest, ponderosa pine forest, and pinyon-juniper woodland. Mixed-conifer forest was found mainly on north-facing canyon slopes and in canyon bottoms; ridgetops and other slopes were dominated by ponderosa pine forest and/or pinyon-juniper woodland.

The Williams study area was located approximately 20 km southeast of Williams, Arizona, in the Sycamore Canyon Wilderness. Sycamore Canyon is a deeply incised drainage with vegetation similar to that on the Chevelon study area. Estimates of relative proportions of different cover types were not available for the Chevelon and William study areas.

Once owls began actively dispersing, they were followed wherever they went. Areas immediately surrounding the main study areas were generally similar in topography and vegetation to those areas. As owls moved more widely, terrain and vegetation became more diverse, ranging from high forested mountains to lowland desert in surrounding valleys.

Capturing and radiotracking owls.—The Coconino study area was shared with an ongoing study of demography of Mexican Spotted Owls (Gutiérrez et al. 1994). All territories in this area were monitored in cooperation with demography field crews to document reproductive status, identify pairs that fledged young, and determine numbers of young fledged. Information on pairs producing young within the other study areas was solicited from forest biologists. We determined the date of fledging to within 7 days for birds on the Coconino study area. All juveniles on the other two study areas were assigned the median fledging date of birds on the Coconino study area for that year.

We captured juvenile owls in August, when their tail feathers were fully grown (beginning approximately 75–80 days after hatching). We captured owls using noose poles (Forsman 1983), and attached radio transmitters (Holohil Systems Ltd., Carp, Ontario) to the central tail feathers using epoxy and dental floss (Guetterman et al. 1991). Transmitters weighed 5–6 g and had an expected battery life of 9–12 months. Because few pairs of owls bred during 1994 and 1995, we attempted to capture all known juveniles in the study areas. Juvenile owls were not sexed because Spotted Owls are monomorphic and sex cannot be determined from plumage characteristics.

Radio signals were received using ICOM (Communications Specialists, Inc., Orange, CA) and Telonics (Telonics, Inc., Mesa, AZ) receivers and a 3-element Yagi antenna. Owl locations were mapped as accurately as possible on USGS topographic maps, and date, time, and Universal Transverse Mercator coordinates were recorded.

From the time of radiotagging through late August, we attempted to locate all radiotagged juveniles visually during the day at least once a week. This schedule was agreed upon with the demography crews to minimize disturbance to the adult owls. By late August the juveniles were more independent and typically roosted away from the adults. At this time we attempted to locate owls 2–3 times per week in anticipation of the onset of dispersal. Once owls initiated dispersal, we attempted to relocate them every 3–4 days and to avoid losing contact with any individual for extended periods of time. When we were unable to efficiently locate all owls from the ground, we initiated aerial tracking flights. Aerial tracking was accomplished as described in Samuel and Fuller (1994). Ground crews attempted to visually locate owls as soon as possible following flights. In most cases ground crews were able to search for owls within 1–3 days of flights. We were not always able to locate owls between flights, however, particularly during periods of rapid dispersal. Information on mortality and the factors responsible was collected opportunistically. Accuracy of aerial locations was checked by visually locating owls from the ground on the same day as the aerial location. Mean distance between aerial and ground locations was 191.4 ± 33.1 S.E. m (range = 0–383 m, n = 15).

Timing of dispersal.—We defined dispersal as the movement of a juvenile owl from its natal area to a new area or succession of areas. We could not precisely define the natal area or the home range of the adult owls and therefore operationally determined

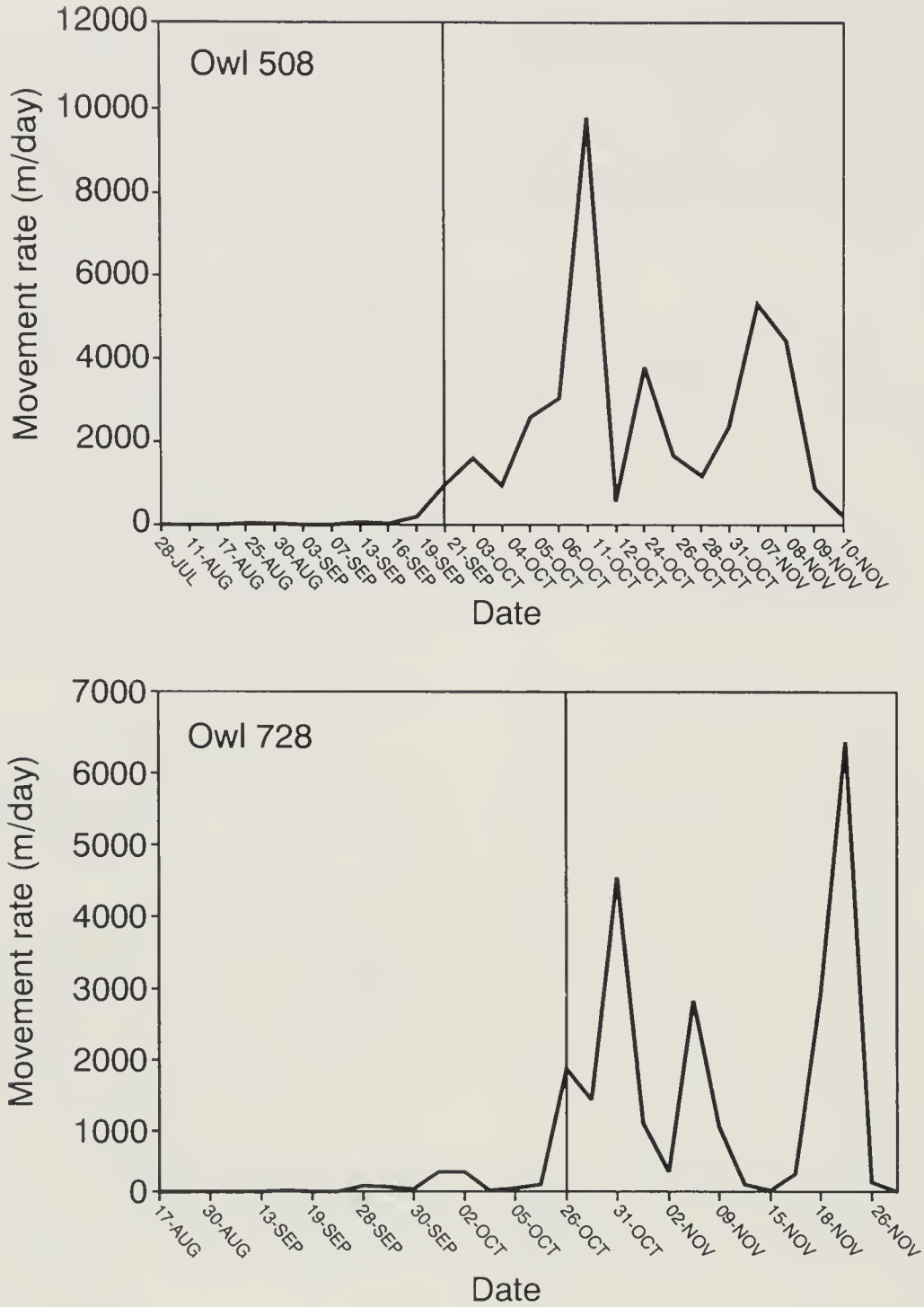

FIG. 1. Movement rates of two radiotagged juvenile Mexican Spotted Owls showing the sudden increase in movement rate indicative of the onset of dispersal. The vertical line indicates the point where dispersal was presumed to have begun. Movement rates were calculated as (distance between successive locations/number of days between those locations). (A) Owl 508; (B) Owl 728.

when dispersal had begun by examining the miminum movement rate between successive locations. All owls that survived to disperse showed a pattern of short-distance movements within the natal area followed by a sudden and dramatic increase in movement rate (Fig. 1). We assumed that dispersal had begun when movement rate abruptly increased above the background level. We assumed that dispersal had ceased when an owl established a territory and paired with a mate. We did not require successful breeding to consider dispersal to have ceased because even established and previously productive pairs of Spotted Owls may not breed in a given year (Forsman et al. 1984).

We estimated time on the natal territory as the number of days between fledging and dispersal. We compared time on the natal territory between years using a Mann-Whitney test (Conover 1980).

Distance and rate of dispersal.—We used locations of dispersing owls to estimate three parameters describing dispersal movements. Final dispersal distance was estimated as the straight-line distance from the nest location to the last known location for a particular

owl. Because some owls moved away from and then returned toward the nest, we also estimated maximum dispersal distance as the distance from the nest to the most distant location recorded for a particular owl. Movement rate (km/day) was estimated as the distance between successive locations divided by the number of days between those locations. We compared final and maximum dispersal distances between cohorts using Mann-Whitney tests. We compared movement rates among individual owls within cohorts using a Kruskal-Wallis test (Conover 1980), using SPSS (ver. 6.1.2) statistical software on an IBM-compatible computer.

Direction of dispersal.—For each dispersing owl with more than five locations following initial dispersal, we calculated the mean direction ($\hat{a}$) of movements during dispersal and the angular deviation ($\hat{s}$) around that mean direction (Zar 1974). We used Rayleigh's z statistic (Zar 1974) to determine whether dispersal movements of each individual were random with respect to direction.

We also estimated the azimuth from the nest location to the final known location for each dispersing owl (final direction). We calculated the mean final direction and the angular deviation around mean final direction for each cohort, and used Rayleigh's z to test for directional pattern within cohorts. All circular analyses were conducted using Oriana for Windows (version 1.01; Kovach Computing Services, Pentraeth, Anglesey, Wales, U.K.).

Habitat use during dispersal.—We recorded information on cover type, type of roost perch (tree, snag, cliff, or other), and roost tree species (for tree roosts) whenever we visually located roosting owls. Cover type was recorded as: mixed-conifer forest, ponderosa pine forest, pine-oak forest, pinyon-juniper woodland, or other. We divided the sampling period into two time intervals for analysis, considering 1 August–31 October to represent a pre- and early dispersal period and 1 November–28 April to represent a later dispersal period. We compared proportional use of cover types and tree species between dispersal periods using multiresponse randomized block procedure (MRBP on an IBM-compatible; Slauson et al. 1991) with individual owl as the blocking variable. This is essentially a distribution-free analog of a blocked analysis of variance with P-values based on permutations of the actual data. Where proportional use differed between dispersal periods, we used MRBP to determine which categories differed significantly. The significance level for multiple comparisons was set at 0.05/k, where k = the number of categories tested. We restricted analyses of habitat use to a subsample of owls (n = 7) that were tracked in both time periods and for which at least 10 roosts were recorded.

Estimating annual survival rates.—We estimated survival rates of juvenile owls over two time intervals each year, and combined these estimates to estimate first-year survival. The first interval covered the period from fledging until we began radiotagging juvenile owls; the second covered the period following radiotagging. Consequently, our estimate of annual survival does not include any mortality that may have occurred between hatching and fledging, but we suspect that mortality is uncommon during this period. Our approach is consistent with previous studies of Spotted Owls, all of which estimated post-fledging demographic rates for owls (e.g., Franklin et al. 1996).

We assumed that juveniles that could not be relocated to radiotag had died and estimated survival from fledging until radiotagging as:

$$\hat{s}_1 = \text{(number juveniles relocated/number fledged)}.$$

We estimated the variance using the normal approximation to the binomial (Zar 1974):

$$\text{var } \hat{s}_1 = [\hat{s}_1 (1 - \hat{s}_1)]/n,$$

where n = number of juveniles fledged. In a few cases on the secondary study areas we were either uncertain about how many owls fledged from a particular nest or were unable to search for the fledglings before late August. These nests were not included in survival estimates for this time period.

We estimated survival rates of radiotagged juveniles ($\hat{s}_2$) using a modification of the Kaplan-Meier (Kaplan and Meier 1958) method developed by Pollock et al. (1989). This method allows for staggered entry (i.e., not all animals are radio-tagged at the same time) and for the use of right-censored data resulting from radio failure or inability to relocate an owl once it dispersed. We used a log rank test to test for equality of survival distributions between cohorts (Pollock et al. 1989).

Because of uncertainty about the fates of some radiotagged owls, we used two models to estimate survival rates. In the first model we censored all individuals for which we could not positively document mortality. We suspected that some of these owls were dead, however, based on the circumstances surrounding transmitter recovery. In the second model we included suspected deaths as mortality events and censored all other birds of unknown fate.

We estimated annual survival of juveniles as ($\hat{s}_1 \times \hat{s}_2$). The variance in survival was estimated following Goodman (1960):

$$\text{var} = [(\hat{s}_1)^2 (\text{var } \hat{s}_2)] + [(\hat{s}_2)^2 (\text{var } \hat{s}_1)] - (\text{var } \hat{s}_2 \times \text{var } \hat{s}_1).$$

Calculation of P-values.—For all analyses we either calculated exact P-values or used a Monte Carlo simulation to estimate P where we could not compute an exact P-value. This method produces an unbiased and reliable estimate (Mehta and Patel 1995). All estimates of variability presented are standard errors unless otherwise noted.

RESULTS

We captured and radiotagged 24 juvenile owls (n = 12 in both 1994 and 1995). Five owls were lost from the sample for various reasons prior to dispersal (Table 1). Two transmitters were located on the ground with tail

TABLE 1. Dispersal dates and fates of radiotagged juvenile Mexican Spotted Owls in Arizona, 1994 and 1995.

Territory	Owl number	Dispersal date[a]	Last date known alive	Fate[b]	Final distance[c]	Maximum distance[d]	Final direction[e]	Mean direction[f]	Angular deviation[g]
Big Springs	809	18 Oct 94	7 Nov 94	RF	0.6	2.1	315.6		
Bonita	469	14 Sep 94	3 Jan 95	RF	17.3	23.5	238.6	80.9	100.7
Bonita	628	9 Sep 94	21 Oct 94	P	7.2	7.7	42.1	228.8	116.9
Circle Bar	937		11 Oct 94	S					
Coyote	659	14 Sep 94	3 Nov 94	S	0.8	22.2	35.8	322.0	132.6
Coyote	748	26 Sep 94	21 Oct 94	S	9.5	20.2	32.3	120.0	129.8
Fain Mtn	492		13 Sep 94	SL					
Fain Mtn	728	16 Oct 94	28 Nov 94	P	47.9	48.4	81.9	326.0	117.2
Lee Butte	508	20 Sep 94	10 Nov 94	S	16.3	25.2	15.4	353.5	143.1
Mayflower	611		15 Aug 94	M					
Serruchos	676	25 Sep 94	13 Oct 94	RF	27.3	28.1	158.9	150.8	99.7
Serruchos	918	20 Sep 94	20 Oct 94	P	53.1	55.7	139.2	285.4	89.3
Bonita	799	9 Oct 95	16 Nov 95	P	60.1	60.5	195.3	14.4	95.9
Hart Cyn	660	20 Sep 95	15 Jun 97	A	5.8	5.8	303.2	60.9	118.1
Hart Cyn	778		20 Sep 95	RF					
Iris	620	5 Sep 95	16 Jan 95	RF	34.9	35.1	155.1	84.7	118.1
Lake Mtn	838	28 Sep 95	5 Feb 96	P	43.0	48.9	289.9	184.5	136.4
Limpios	857	12 Sep 95	26 Apr 96	SL	72.1	73.5	269.3	55.1	110.4
Mahan Mtn	697	23 Sep 95	3 Oct 95	SL					
Mayflower	599	6 Oct 95	10 Oct 95	RF	29.4	29.4	214.8		
Mayflower	877	6 Oct 95	11 Oct 95	SL	16.5	16.5	201.3		
Mint Spring	640	18 Sep 95	2 Oct 95	SL					
Station	678	30 Sep 95	20 Nov 95	SL	3.4	18.3	142.2	162.8	107.4
Station	739		20 Sep 95	RF					

[a] Owls with no dispersal date were lost from the sample prior to dispersing.

[b] Explanatory notes for fates: RF = radio found, fate unknown; P = found dead, probable predation; S = found dead, probable starvation; SL = signal lost, fate unknown; M = molted tail feathers with attached radio; A = alive and paired.

[c] Straight-line distance (km) from the nest to the last location where the owl was observed alive or found dead. Not calculated for owls lost from the sample prior to dispersal, or for owls with fewer than 5 relocations following initiation of dispersal.

[d] Straight-line distance (km) from the nest to the location farthest from the nest. Not calculated for owls lost from the sample prior to dispersal, or for owls with fewer than 5 relocations following initiation of dispersal.

[e] Direction (°) from the nest to the last known location for an individual owl. Not estimated for owls lost from the sample prior to dispersal.

[f] Mean direction (°) of all post-dispersal movements for an individual owl. Calculated following Zar (1974); not calculated for owls with fewer than 5 post-dispersal relocations.

[g] Angular deviation around the mean direction for an individual owl. Calculated following Zar (1974); not calculated for owls with fewer than 5 post-dispersal relocations.

feathers attached and no signs of predation. We were able to verify that at least one of these radios was lost through premature molt by resighting the bird on its natal area. One owl was found dead in the natal area, and we lost the signal on another owl. For the latter owl, we are uncertain whether the radio failed or whether this owl dispersed and we were unable to locate it. The transmitter from the fifth owl was tracked to a large burrow beneath a stump. This could indicate predation. We cannot rule out scavenging following death for another reason, however, or premature molt followed by an animal dragging the radio and attached tail feathers into a burrow.

The remaining 19 owls (9 in 1994 and 10 in 1995) all dispersed from the natal area; no owls were observed to remain in their natal area. Only one owl was tracked until it settled in a territory. This 1995 juvenile moved 5.8 km downstream from its natal area along a major drainage to an historically occupied, but currently vacant, territory immediately adjacent to its natal area. The juvenile settled in this area in early October 1995 and had obtained a mate by June 1996. The mate appeared to be a 1-yr old female based on appearance of the retrices (Moen et al. 1991) and her vocalizations. This pair did not nest in 1996 but nested successfully in 1997.

One other owl was monitored through late April. This owl traveled extensively for two months following initial dispersal. It "settled" into a defined area of approximately 670 ha sometime between 22 November and 12 December 1995, and remained in this area

through 26 April 1996. We lost the signal from its transmitter at that time and are uncertain whether it moved on or the radio failed. The area in which this bird settled was a canyon dominated by pinyon-juniper woodland (elevation approximately 1400 m).

All other owls either died or were lost from the sample at various times because of radio failure or inability to relocate the owl.

Timing of dispersal.—We were able to pinpoint dispersal dates of individual owls to ±3.7 days in 1994 (range = 1–9 days) and ±2.7 days in 1995 (range = 0–6 days). All owls dispersed between 9 September and 18 October in 1994, with 66.7% dispersing in September (Table 1). In 1995, all owls dispersed between 5 September and 9 October, with 70% dispersing during September.

Time spent on the natal area differed significantly between cohorts (Mann-Whitney test: Monte Carlo $P = 0.048$). Owls spent an average of 101 ± 4.8 days (range = 87–125 days) on the natal area in 1994 versus 86.8 ± 3.4 days in 1995 (range = 73–102 days). Most of this difference appeared to be attributable to only five owls. Two owls dispersed relatively late in 1994 (16 and 18 October), and three owls fledged during July in 1995, considerably later than normal for Mexican Spotted Owls (Rinkevich et al. 1995). Although these three owls were the last to disperse in 1995, all dispersed by 9 October (Table 1).

Distance and rate of dispersal.—Neither final nor maximum dispersal distance differed significantly between cohorts (Mann-Whitney tests: $P > 0.05$ for final and maximum dispersal distances). Median final dispersal distance for all owls was 16.9 km (range = 0.6–72.1 km); median maximum dispersal distance was 25.2 km (range = 2.1–73.5 km). Because only one owl was tracked until it settled and paired, we suggest that these distance estimates should be viewed as minimum estimates of dispersal capability.

Movement rates during dispersal differed significantly among owls within cohorts (Kruskall-Wallis test: Monte Carlo P-values = 0.002 for 1994, 0.006 for 1995). Movement rates also varied considerably over time for individual owls, with periods of rapid movement interspersed with periods when owls were relatively sedentary (Fig. 1). Mean and maximum movement rates of 19 individual owls ranged from 148.3–3,053.3 and 303.3–13,442.4 m/day, respectively. Because owls were not relocated daily, considerable movement likely went undetected between relocations, and estimates presented here almost certainly underestimate actual movement rates.

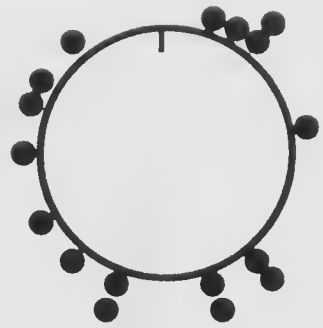

FIG. 2. Circular scattergram showing final directions from the nest to the last known location for 17 radiotagged juvenile Mexican Spotted Owls in Arizona in 1994 and 1995. Each dot represents one individual ($\hat{a}$ = 195°, r = 0.093).

Direction of dispersal.—The mean directions of movement were not significant for any of the 14 owls (Rayleigh's Z: all $P > 0.05$), suggesting that movements of individual owls were not significantly concentrated around the mean direction for that individual. This was borne out by direct observation. Individual owls moved directionally at times, but these movements were interspersed with periods of wandering and/or complete reversals of travel direction.

There was no significant directional pattern to movements for either cohort, based on directions to final locations for individuals (1994: $\hat{a}$ = 51.3°, $\hat{s}$ = 82.3°, $P > 0.05$; 1995: $\hat{a}$ = 219.7°, $\hat{s}$ = 60.3°, $P > 0.05$). Because mean final direction did not differ from random for either cohort, we pooled cohorts for estimation of overall mean direction ($\hat{a}$ = 195.8°, $\hat{s}$ = 124.7°; Fig. 2).

Habitat use during dispersal.—We recorded perch type at 164 roost sites. Most roosts (90.0%) were in live trees, but snags (5.0%), cliffs (1.9%), and other perches such as stumps and logs (3.1%) were also used. Overall use of cover types differed significantly between early and late dispersal periods [P = 0.021, n = 7 owls (111 roost sites)], but use of individual cover types did not differ significantly [$P > 0.01$ (=0.05/5)] between dispersal periods in Bonferroni-controlled multiple comparisons (Fig. 3). We were not able

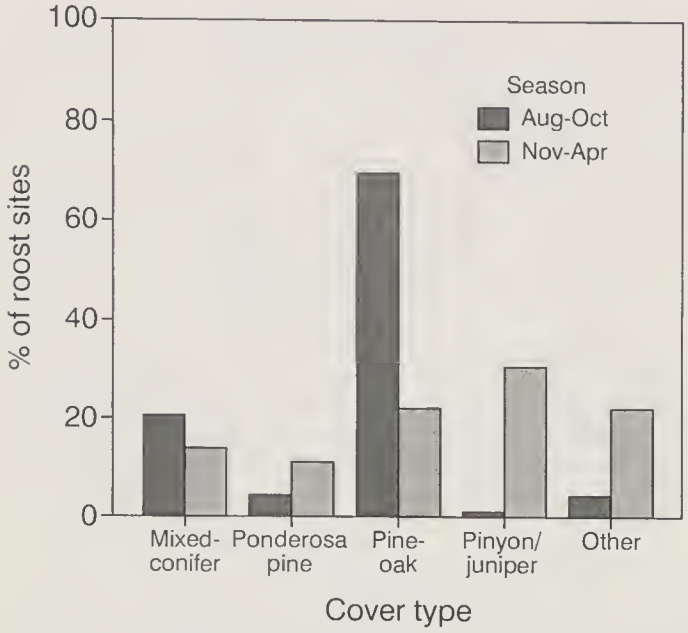

FIG. 3. Cover types used for roosting by seven juvenile Mexican Spotted Owls during dispersal. Based on 45 and 66 roost sites sampled during early and late dispersal periods, respectively. Overall use of cover types differed significantly between time periods, but use of individual cover types did not ($P > 0.01$, Bonferroni adjustment).

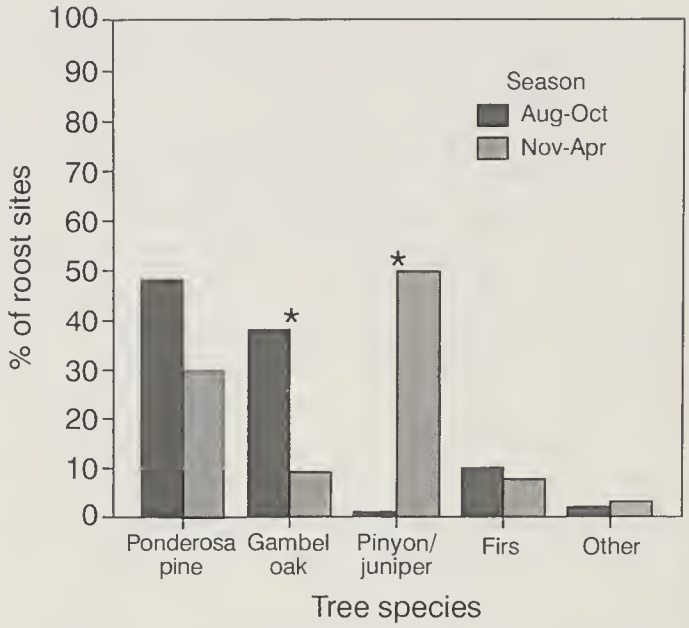

FIG. 4. Tree species used for roosting by seven juvenile Mexican Spotted Owls during dispersal. Based on 45 and 66 roost sites sampled during early and late dispersal periods, respectively. The category "firs" includes Douglas-fir and white fir. Significant differences ($P < 0.01$) indicated by asterisks.

to quantify relative availability of cover types within the areas traversed by owls, so we cannot compare habitat use to availability. In the late-dispersal period, owls roosted at significantly lower elevations than during the early-dispersal period (MRBP: $\bar{x}$ = 1,753 ± 44.4 m vs. 2,177 ± 25.4 m, P = 0.017), which is consistent with the observed differences in cover types used between periods.

Proportional use of roost tree species also differed significantly between early and late dispersal periods (P = 0.02). Relative to the early dispersal period, owls roosted in Gambel oak significantly less often (P = 0.004) and in pinyon pine and junipers (P = 0.01) significantly more often in the late dispersal period period (Fig. 4). Given the observed variation in use of cover types between dispersal periods, differences in tree species used may have reflected patterns of relative availability of trees.

Survival rates.—Survival was relatively high during the period between fledging and the onset of radiotagging activities during both years ($\hat{s}_1$; Table 2). We may have underestimated survival if any owls were alive but unlocated. Because juveniles are typically found with the adults and/or their siblings at this time (Rinkevich et al. 1995) and thus easily located, such underestimation is unlikely.

Kaplan-Meier estimates of survival rates for radiotagged owls ($\hat{s}_2$; Table 2) differed between cohorts in both models used (log rank test: P = 0.043 and 0.034 for models 1 and 2, respectively). Estimates of mean survival time for the 1994 and 1995 cohorts, respectively, were: model 1: 98.7 ± 14.1 vs. 270.2

TABLE 2. Estimated survival rates of radiotagged juvenile Mexican Spotted Owls in Arizona, 1994 and 1995.

Cohort	n	Model[a]	$\hat{s}_1$[b]	$\hat{s}_2$[c]	Annual survival[d]	95% confidence interval[e]
1994	12	1	0.833	0.173	0.144	0.000–0.957
		2	0.833	0.101	0.084	0.000–0.241
1995	13[f]	1	0.923	0.556	0.513	0.032–0.994
		2	0.923	0.486	0.449	0.000–0.900
Both	25	1	0.880	0.326	0.287	0.000–0.751
		2	0.880	0.233	0.205	0.000–0.561

[a] Model 1 censored all owls with unknown fates; model 2 assumed that owls with transmitters tracked to burrows were dead.
[b] Survival from date fledged through date radiotagged.
[c] Survival from date radiotagged until bird died or was censored.
[d] Annual survival = ($\hat{s}_1 \times \hat{s}_2$).
[e] Confidence intervals for annual survival computed using equation 4 from Pollock et al. (1989).
[f] Includes one owl that was alive at beginning of radiotagging operations but not captured and radiotagged.

± 58.9 days; model 2: 85.9 ± 10.9 vs. 242.4 ± 57.7 days.

Eight owls (33.3%) were confirmed dead, with another four (16.7%) suspected to be dead (radios found in burrows). Three owls found dead were emaciated and appeared to have starved. In the other five cases transmitters were found among piles of feathers and bones, suggesting predation as the cause of death. Great Horned Owl (*Bubo virginianus*) feathers were found under a tree near one recovered transmitter, but we were unable to positively identify the predator responsible. In fact, we cannot be certain that these cases represent predation, as we cannot rule out scavenging following death from other causes. It is also possible that disease or injury could have predisposed birds to death from predation or starvation. For example, one bird that apparently starved suffered an obvious eye injury approximately two weeks before dying. It appeared to become lethargic following the injury, which may have reduced its ability to hunt or avoid avian predation effectively.

DISCUSSION

Dispersal behavior.—Our attempt to monitor dispersal behavior of juvenile Mexican Spotted Owls met with limited success. Because we were able to track only one owl until it settled and paired, we are unable to comment meaningfully on the process of natal dispersal (e.g., Greenwood et al. 1979) for this owl. We are also unable to comment meaningfully on dispersal distance for the same reason. Thus, our results primarily document timing of dispersal, movement patterns, and habitat use of juvenile owls during dispersal.

With respect to timing of dispersal and movement patterns, our results were generally consistent with other studies on all three subspecies of Spotted Owls (Forsman et al. 1984, Gutiérrez et al. 1985, Laymon 1988, Miller 1989, Willey 1995, Hodgson and Stacey 1996). All owls dispersed from natal areas over a 4–5 week period in September and October. Initial dispersal movements tended to be rapid and abrupt (Fig. 1). Rapid movements sometimes continued for a period of several days or weeks interspersed with periods when owls were more sedentary. Individual owls moved directionally at times, but more often wandered or even reversed direction, and there was no significant directional pattern to movements of either cohort.

Dispersing juveniles were located in a variety of habitats ranging from high-elevation forests to pinyon-juniper woodlands and riparian areas surrounded by desert grasslands. Some juveniles remained in forests similar to typical Spotted Owl breeding habitat. For example, the juvenile that settled in an historic territory consistently roosted within the historic nest grove, suggesting that even inexperienced juveniles recognize typical breeding habitat when they encounter it. In contrast, four other juveniles that were monitored beyond mid-November moved down in elevation, with at least two establishing apparent home ranges, on which they were repeatedly located over a period of several months, in pinyon-juniper woodlands. These woodlands were very different in habitat composition and structure from known breeding habitat of Mexican Spotted Owls. This may indicate that dispersing owls were not assessing habitat suitability in the context of typical breeding habitat. Some dispersing owls settled and survived in these atypical habitats for considerable periods, and some adult Mexican Spotted Owls migrated to pinyon-juniper woodlands during the winter (Ganey et al. 1992, Rinkevich et al. 1995). Thus, some habitats not suitable for breeding may have met the needs of this owl during the nonbreeding season. If so, modeling habitat connectivity for Mexican Spotted Owls based solely on the distribution of typical breeding habitat may be inappropriate. Thomas and coworkers (1990) also recognized that habitats not suitable for breeding could meet the needs of dispersing owls, and explicitly incorporated "dispersal" habitat in their proposed conservation strategy.

Population models incorporating dispersal behavior in Northern Spotted Owls (Thomas et al. 1990, Lamberson et al. 1994; see also Doak 1989) have assumed, either explicitly or implicitly, that dispersing owls move randomly, evaluate habitats as they encounter them, and settle in the first vacant habitat of suitable quality. This is a highly efficient search pattern and model results depend strongly on this pattern (Thomas et al. 1990, Harrison et al. 1993, Lamberson et al. 1994). Our results were equivocal with respect to how well these models describe the behavior of dispersing

owls. Most of the owls we monitored appeared to move randomly, but also appeared to move too rapidly to be assessing either habitat quality or occupancy status of areas traversed (see also Hodgson and Stacey 1996). However, most of these owls died. The one successful disperser we monitored used a dispersal strategy consistent with these models.

The timing of dispersal in Spotted Owls also seems to present problems in terms of assessing habitat occupancy. Calling rates of Ural (*S. uralensis*) and Eastern Screech-Owls (*Otus asio*) increase during the dispersal period (Lundberg 1980, Ritchison et al. 1988), possibly to advertise occupancy status and discourage dispersing juveniles from attempting to settle in an occupied area (Lundberg 1980, Belthoff and Ritchison 1989). In contrast, vocalizations of Mexican Spotted Owls declined in frequency during the dispersal period (Ganey 1990). Further, the adults begin to wander more widely during this period and are sometimes located considerable distances from nest areas (Ganey and Balda 1989). Thus, dispersal in Mexican Spotted Owls occurs at a time when it may be difficult for juveniles to accurately assess ocupancy status of suitable habitat.

Survival estimates.—Our estimates of first-year survival of juvenile owls fall within the range reported in studies of Northern and California Spotted Owls (Gutiérrez et al. 1985, Miller 1989, Noon et al. 1992, Burnham et al. 1996), are close to the estimate based on resightings of banded birds on the Coconino study area (28.6 ± 7.9%; White et al. 1995), and are consistent with high mortality rates reported for first-year individuals of Spotted and other owls (Southern 1970, Forsman et al. 1984, Gutiérrez et al. 1985, Korpimäki and Lagerstrom 1988, Laymon 1988, Belthoff and Ritchison 1989, Miller 1989). These estimates for Mexican Spotted Owls should be viewed as preliminary, however, for several reasons. First, fate was unknown for 58% of the radiotagged owls. Although the Kaplan-Meier estimator is able to handle right-censored data resulting from radio failure or inability to relocate owls (Pollock et al. 1989), the number of owls for which fate was unknown still argues for cautious use of survival estimates. Second, initial sample sizes were small, resulting in large confidence intervals around survival estimates. Third, variability among years was significant (Table 2). Based on these factors, we suspect that tracking of hundreds of owls over at least 10 years will be required to accurately and precisely estimate annual survival rates of juvenile owls.

The pronounced difference in survival estimates between time intervals in both years might suggest that radiotagging juvenile owls negatively affects their survival. Although we cannot rule out an effect of radiotags on survival, we suspect that such an effect was small if it existed at all. Mortality of radiotagged owls was minimal until they initiated dispersal, at which time mortality increased dramatically. Consequently, we suspect that the high mortality rate observed among radiotagged owls was due to the rigors of dispersal rather than to the effect of carrying a radio.

Predation and starvation appeared to be important causes of juvenile mortality during dispersal (see also Hirons et al. 1979, Forsman et al. 1984, Gutiérrez et al. 1985, Miller 1989). The prevalence of starvation could be due to the relative inexperience of dispersing juveniles, coupled with the difficulties of foraging in unfamiliar terrain. Predation risks may also be greater for owls travelling through unfamiliar terrain, and particularly for owls undergoing nutritional stress (Hirons et al. 1979).

Conclusions.—Better information on dispersal patterns, habitat use, and survival rates of juveniles is clearly needed. Until such information is available, our ability to model population dynamics and/or habitat connectivity will be limited. Our attempts to gather reliable information on these aspects of the ecology of Mexican Spotted Owls met with limited success. Problems with premature molt of tail feathers [also documented by Reid et al. (1996)] and suspected radio failure limited our ability to follow birds for extended periods and/or to positively determine their fate. Problems with premature molt could be addressed by attaching radios using backpack harnesses, but there is concern over the effects of backpack radios on Spotted Owls in general (Paton et al. 1991, Foster et al. 1992) and on juvenile owls in particular. These problems suggest that hundreds of owls may need to be radiotagged to ensure that adequate numbers are tracked successfully. The pronounced differ-

ence in survival estimates between years suggests that long-term studies will be required.

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THE INFLUENCE OF STARLINGS ON FLICKER REPRODUCTION WHEN BOTH NATURALLY EXCAVATED CAVITIES AND ARTIFICIAL NEST BOXES ARE AVAILABLE

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ABSTRACT.—I monitored 54 pairs of Northern Flickers (*Colaptes auratus*), with artificial nest boxes placed near their nest cavities, during three breeding seasons in Ohio to determine whether such boxes would help reduce nest-site competition by European Starlings (*Sturnus vulgaris*). Twenty-seven of 40 flicker pairs in the presence of starlings (68%) lost a total of 42 cavities to starlings in spite of the presence of a nearby flicker nest box, and nine of these pairs lost two or more cavities to starlings. Thus, the presence of nest boxes did not appear to help nesting flickers and in fact may have deterred them by attracting additional starlings. During initial nest attempts, flicker pairs without starlings produced larger clutches, more nestlings and more fledglings than flickers with starlings. Flicker pairs without starlings were not adversely affected by the presence of a nearby nest box and 64% of such pairs eventually fledged young from their excavated nest cavities. Conversely, no pairs without starlings and only one pair with starlings opted to nest in a nest box versus their excavated or renovated nest cavity. Only 3 of 40 starling pairs opted to nest in a box when excavated flicker cavities were available. However, starlings eventually fledged young in only 9 of the 42 flicker cavities they usurped (21%).
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For several decades it has been documented that European Starlings (*Sturnis vulgaris*) usurp nest cavities from a variety of woodpecker species (Wood 1924; Shelley 1935; Bent 1939; Howell 1943; Dennis 1969; Erskine and McLaren 1976; Jackson 1976; Troetschler 1976; Short 1979, 1982; Weitzel 1988; Ingold 1989, 1994; Kerpez and Smith 1990), as well as from several secondary cavity-nesting species (Bent 1950, Zeleny 1969, Erskine and McLaren 1976, Feare 1984, Ingold and Ingold 1984). Ingold (1989) found that Red-bellied Woodpeckers (*Melanerpes carolinus*) nesting in the presence of starlings suffered reductions in their reproductive output as a result of starling harassment. Northern Flickers (*Colaptes auratus*), one of the largest woodpeckers in North America, are also commonly harassed by starlings (Kilham 1959, Sedgwick and Knopf 1990, Ingold 1994, Moore 1995). Moore (1995) suggested that although flickers frequently lose nest cavities to starlings early in the season, they often renest after starlings have completed initiating nest attempts. Since very few flicker nest cavities are usurped by starlings late in the season (Ingold 1994, Moore 1995), it may be that late-nesting flickers do not suffer reductions in fecundity as a result of starling harassment (see Ingold 1994). Ingold (1996), however, showed that late-nesting flickers in Ohio produced significantly smaller clutches, as well as fewer nestlings and fledglings compared to early-nesting flickers. Moreover, most of the successful early-nesting flicker pairs were those able to avoid starling competition. Ingold and Densmore (1992) and Ingold (1994) found that when flickers, Red-bellied Woodpeckers and Red-headed Woodpeckers (*M. erythrocephalus*) nesting in areas of starling overlap were forced to delay nesting, they often returned to nest in their original cavity or to another in the same tree.

Northern Flickers are sometimes considered weak excavators (Harestad and Keisker 1989, Winkler et al. 1995) and have been known to use wooden nest boxes for nesting (Bent 1939, Bower 1995). An inadequate supply of suitable nest sites limits the reproductive success of cavity-nesting birds (see Cline et al. 1980, Mannan et al. 1980, Nilsson 1984, Raphael and White 1984, Li and Martin 1991). When this occurs a nest box placed near a flicker nest cavity could provide a suitable alternative nest site for flickers or starlings competing for a flicker cavity. Gutzwiller and Anderson (1986) found that when suitable nest cavities were abundant, woodpeckers occasionally nested in the same tree at the same time with European Starlings. Ingold (1990) also reported Red-headed and Red-bellied

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woodpeckers nesting in the same tree simultaneously with starlings.

In this study I placed a nest box designed for flickers (see Bower 1995) near all active flicker nest cavities early in the nesting season to determine if either starlings or flickers would take up residency in the box, thus conceding to the other species the flicker nest cavity. Since numerous studies have already documented that flickers lose excavated nest cavities to starlings (Sedgwick and Knopf 1990; Ingold 1994, 1996; see also Moore 1995), I did not compare flicker nest sites with and without boxes; rather, all sites had boxes and I compared sites with and without starlings. I then tested the null hypotheses that when nest boxes are established near active flicker nests there is no difference in the reproductive success of flickers nesting in the presence of starlings versus flickers nesting in the absence of starlings, and that there is no difference in the timing of nesting between flickers with and without starlings.

STUDY AREA AND METHODS

From late March through late July 1994–1996, I located active Northern Flicker nest cavities in and around New Concord, Muskingum Co., Ohio. Flicker nests were located most frequently in open woodlands and agricultural areas, but were also found in forested and residential areas (see Ingold and Densmore 1992, Ingold 1994 for a more detailed description of the study area).

Flickers were categorized as either being in the presence or absence of starlings. Pairs were considered to be starling-free if I did not detect starlings in a 0.25 ha circular plot around their nest cavity throughout the nesting season (see Ingold 1989, 1994). Although this method of categorization is not fool proof, since most flickers I considered to be starling-free were found in more forested areas and because I monitored all nest sites at least once and frequently twice a week, the criterion used to define such pairs is fairly sound. I erected a nest box designed for flickers similar to the one described by Bower (1995) within 0.5–2.0 m of all active flicker cavities (both with and without starlings) that were still being excavated or in which flickers had begun egg laying. Depending on the diameter of the tree and the height of the cavity, boxes were attached either above, below, or in some instances beside the cavity ($\bar{x}$ height of boxes = 6.5 m; n = 41). Boxes were oriented so that the entrance was facing in about the same direction as the entrance of the flicker cavity. I did not attach a nest box next to active cavities in which the flicker nesting effort had progressed to the incubation or nestling stage, since by this point most flicker pairs were not in danger of losing their cavities to starlings. During 1994 I placed cedar woodchips or planer shavings at the bottom of each nest box to encourage flicker occupancy. During 1995–1996 I filled the boxes up to the cavity entrance with cedar woodchips to further encourage flicker use (see Bower 1995).

I monitored each nest box and active woodpecker nest cavity for a minimum of 30 min each week between 07:30 and 18:00 EDT to determine their status and to detect possible starling/flicker interactions. Nest sites at which flickers and starlings were both present were monitored up to 90 min each week. Because I was seldom at a nest site when starlings took over, I considered a flicker cavity to be usurped when two criteria were met: (1) if I observed starlings in the cavity or if there was evidence that starlings occupied the cavity (such as fecal material around the cavity entrance and/or grass and leaves inside the cavity), regardless of whether or not they subsequently nested in the cavity, and (2) if the flicker pair did not return to occupy the nest cavity within a two week period after the date recorded for the initial takeover. Flicker cavities and nest boxes that became inactive for more than four consecutive weeks during the study were not monitored during the remainder of the nesting season. Starlings that initiated nest attempts in boxes after having usurped a flicker cavity, were allowed to continue nesting if the flickers were subsequently detected in the same ~1.0 ha circular plot around the cavity tree, to ascertain whether the flicker pair would return to their original nest cavity.

A total of 41 nest boxes were erected during the study (20 in 1994, 14 in 1995, 7 in 1996). In some instances flicker pairs lost multiple cavities to starlings in the same cavity tree during the same year. In such instances, I erected a new nest box next to each new flicker cavity and treated it as a new observation. Thus, some snags or cavity trees had more than one nest box attached to them. Previously excavated flicker nest cavities or boxes that were used by flickers in subsequent years (n = 13) were also treated as new observations. Data were collected from a total of 54 flicker pairs during the three-year period (16 in 1994, 25 in 1995, 13 in 1996).

Using a 10-m extension ladder, I climbed to those active flicker cavities that I could reach once or twice weekly and examined the contents with a light and mirror. I considered the clutch size to be the number of eggs present at the onset of incubation. I considered the number of nestlings to be the number of eggs that hatched regardless of the number of nestlings that eventually fledged. I considered the number of fledglings to be the number of nestlings that were present in the cavity upon my last visit (see Ingold 1996).

Because the number of flicker nests from which I obtained clutch sizes, nestling numbers, and fledgling numbers was small (n = 3, 4, and 2 nests without starlings and 7, 9, and 5 nests with starlings from 1994–1996 respectively), I pooled these data across years. Once pooled, I divided clutches into early nests (those completed before 1 June, the date by which at

least 90% of uninterrupted flicker pairs had initiated their first clutch) and late nests (completed after 1 June, by which time second nest attempts were common, usually as the result of a failed first nest attempt; see Ingold 1996). I used *t*-tests to test for differences in clutch size, nestling numbers, and fledgling numbers between nests with and without starlings, and between early and late nests; however, in several instances in which the data were not normally distributed, I used Mann-Whitney Rank Sum Tests. All statistical analyses were performed with Sigma Stat, ver. 1.0 on a PC computer.

The number of flicker cavities usurped by starlings was small, and the number of cavities usurped relative to the number of cavities that were available varied only minimally among years. Thus, these data were pooled. I used a regression analysis to determine if the number of flicker cavities usurped relative to the number of cavities that were available was associated with the progression of time.

Differences in the timing of nest excavation, incubation, and the presence of nestlings and fledglings in flicker pairs with and without starlings were tested among years using Kolmogorov-Smirnov tests. Because no differences were detected ($P > 0.05$) and since my sample sizes were relatively small (3, 8, and 3 pairs without starlings and 13, 17, and 10 pairs with starlings from 1994–1996 respectively), I pooled these data.

RESULTS

Flicker response.—Nest starts by flicker pairs both in the presence and absence of starlings occurred from mid-April through early May (Fig. 1). Thirteen flicker pairs with starlings (32.5%) were still excavating nest cavities during the final week of May, compared to 2 flicker pairs without starlings (14.3%; Fig. 1). Although this difference is not significant ($\chi^2 = 3.16$, df = 1, $P > 0.05$), a significantly greater proportion of flicker pairs with starlings versus without starlings ($\chi^2 = 9.21$, df = 2, $P < 0.05$) were still rearing nestings in June and July (Fig. 1). Twelve of 14 flicker pairs without starlings (86%) produced clutches in their original nest cavities while none undertook a nest attempt in a nearby nest box instead of their nest cavity. Nine flicker pairs without starlings (64%) eventually fledged at least one young during their first nest attempt.

Twenty-seven of 40 flicker pairs in the presence of starlings (68%) lost their nest cavities to starlings despite the presence of nearby nest boxes. Of these, 18 flicker pairs appeared to have lost no more than one cavity each to starlings, six pairs lost at least two cavities to starlings, one pair lost three cavities, one pair lost four cavities and one pair lost five cavities. A significantly smaller proportion of flicker pairs with starlings fledged young during their initial nest attempt versus pairs without starlings (8 of 40 vs 5 of 14 respectively; 20% vs 36%; $\chi^2 = 7.49$, df = 1, $P < 0.01$). Flicker pairs without starlings produced significantly larger clutches than pairs with starlings ($t = 2.16$; df = 28; $P < 0.05$); mean nestling and fledgling numbers of pairs without starlings were also

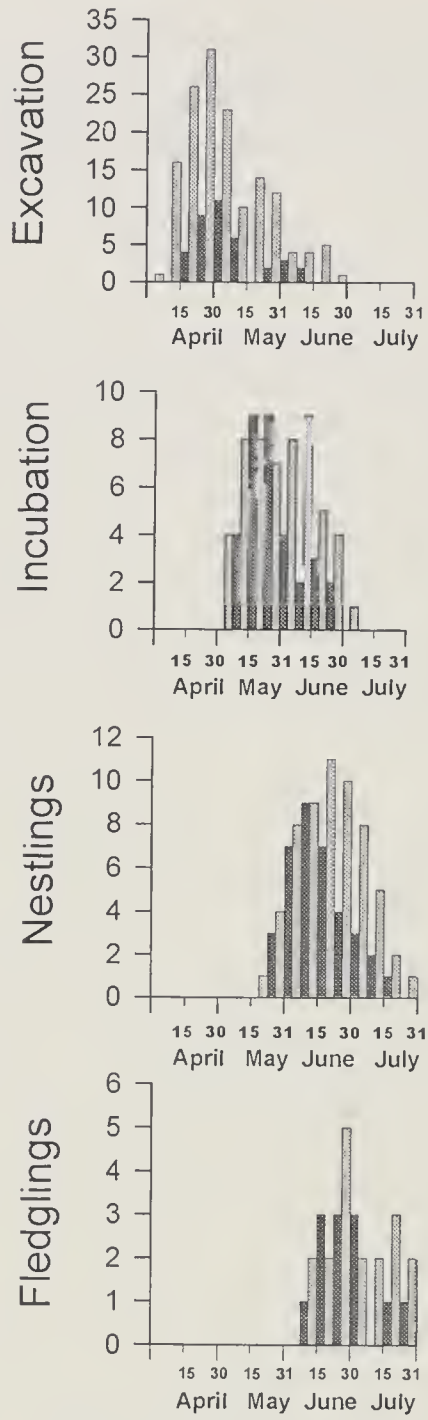

FIG. 1. Nesting pheonology of flicker pairs with boxes in the presence (light bars) and absence (dark bars) of starlings during 1994–1996 (n = 14 and 40 respectively; weeks on x-axis; number of flicker pairs on y-axis).

TABLE 1. Comparison of the reproductive success of flicker pairs in the presence and absence of starlings. Because of small sample sizes, reproductive data for all three years were combined. Differences in clutch sizes, nestling numbers and fledgling numbers were examined using *t*-tests.

	Starlings absent			Starlings present			
Variable	*n*	Mean	SD	*n*	Mean	SD	*P*-value
Clutch size	9	7.44	2.24	21	5.43	2.38	0.039
Nestlings produced	9	5.56	2.46	21	3.86	2.76	>0.05
Fledglings produced	9	3.78	2.99	21	2.57	2.64	>0.05

larger than pairs with starlings, but not significantly so (Table 1). When I divided flicker clutches into early versus late nests, clutch size, nestling numbers and fledgling numbers from early nests were significantly larger than those from late nests ($P < 0.05$ in each case; Table 2). Moreover, at least 90% of late-nesting flicker pairs encountered starling harassment early in the nesting season. Only one experimental flicker pair undertook a nest attempt in which eggs were laid in the nearby nest box. This particular pair lost its excavated nest cavity to starlings and moved to the nest box where they eventually fledged four young. The starlings at this location abandoned the excavated nest cavity they usurped and disappeared from the area.

With the progression of time, the number of flicker cavities usurped by starlings decreased significantly ($F = 26.8$, $P < 0.001$, df = 1,8; Fig. 2). At least 10 of 27 flicker pairs (37%) that lost cavities to starlings in April and early May returned to nest in the same 0.25 ha circular plot, often in the same tree or nest cavity, in late May or June.

Starling response.—Starlings used a nest box at only 3 of 40 flicker nest sites (7.5%) rather than attempt to usurp the flicker nest cavity or move elsewhere to nest. In each instance, both the starlings and flickers successfully fledged young from nests in close proximity to each other. At 10 flicker cavities (25%) starlings neither usurped the active flicker cavity nor used the nest box, and at five of these locations (50%) the flicker pair eventually fledged young. Starlings laid eggs in at least 15 of the 42 (36%) flicker cavities they usurped but fledged young in only nine (21%). At eight of the usurped cavities (19%), starlings subsequently laid eggs in the nearby nest box rather than in the cavity, and in four instances (9.5%) they laid eggs in both the usurped nest cavity and the nearby flicker nest box. In all of the latter four instances more than one starling pair was involved.

Interspecific use of nest-box trees.—At 13 nest-box locations, two or more different species undertook nest attempts (in which eggs were laid) in the nest box and/or in cavities in the same tree at the same time. At five locations, one pair of flickers and one or more pairs of starlings were undergoing egg-laying or incubation at about the same time. In three instances, starlings used the nest box while flickers used a nearby cavity; in all three instances both the starlings and flickers fledged young. At a fourth location, a pair of incubating flickers lost their nest cavity to starlings, while a pair of starlings had eggs in the nearby nest box. It was unclear whether it was the starling pair with eggs that usurped the nearby flicker nest cavity or another starling

TABLE 2. Comparison of the reproductive success of early-nesting flickers (clutches completed before 1 June) and late-nesting flickers (clutches completed after 1 June). Because of small sample sizes, reproductive data for all three years were combined. Because the data did not meet the assumption of normality, they were examined using Mann-Whitney Rank Sum tests.

	Early nesting Flickers			Late nesting Flickers			
Variable	*n*	Mean	SD	*n*	Mean	SD	*P*-value
Clutch size	22	7.18	2.08	9	4.56	2.07	0.003
Nestlings produced	22	4.86	2.96	10	3.20	2.30	0.048
Fledglings produced	22	3.64	2.77	10	1.70	2.26	>0.05

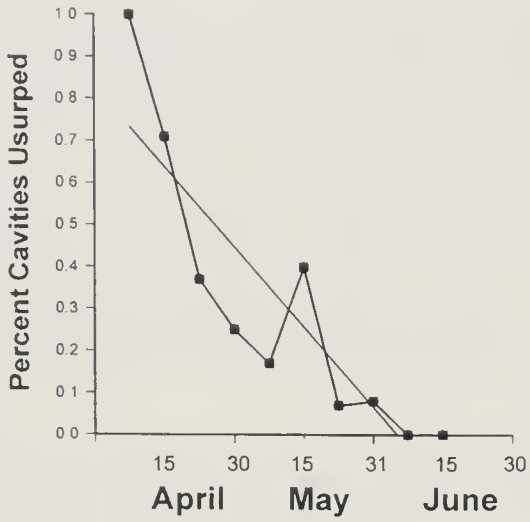

FIG. 2. The relationship between time and the proportion of flicker cavities usurped by starlings (Least Square fit: $Y = 7.96 - 8.08\times$; $r^2 = 0.770$; $P < 0.001$) during 1994–1996.

pair. At a fifth location in late May 1995, I found three flicker eggs and two starling eggs in the same flicker cavity at the same time. A week later all the eggs were gone; starlings returned within a few days, however, and initiated a new clutch in the flicker cavity.

At five locations, a pair of flickers and a pair of Red-headed Woodpeckers nested in the same tree simultaneously. In four instances, both species successfully fledged young, and in the process, generally did not interact with each other. At two of these locations the flicker and Red-headed Woodpecker pairs did not complete nesting until mid- to late July as a result of starling harassment earlier in the nesting season. In no case did either species use a nest box rather than an excavated nest cavity.

At one of the 13 locations of simultaneous interspecific use, a pair of American Kestrels (*Falco sparverius*) laid eggs in the flicker nest box while several pairs of starlings were incubating clutches in the same snag. Within a week the kestrel clutch disappeared and starlings had built a grass nest inside the box. At another location, starlings and Red-headed Woodpeckers nested in the same snag at about the same time and both successfully fledged young in June. I witnessed only a few competitive interactions at this location between these species. At the thirteenth location I found 7–8 pairs of nesting starlings, one pair of Pileated Woodpeckers (*Dryocopus pileatus*) and one pair of nesting flickers in the same snag at the same time. Most of the starlings, including occupants of the nest box, fledged young at this location by the end of June. The pileated pair fledged offspring during the first week of June, apparently without encountering any starling harassment. The flicker pair lost five nest cavities to starlings from late April through mid-June before successfully undertaking a nest attempt in late June. The pair eventually fledged young in late July in one of the nest cavities that starlings had usurped earlier in the season.

DISCUSSION

Flicker response to boxes.—Based on the prevalence and intensity of starling/flicker nest-site competition in this study, it appears that suitable nest cavities were in short supply; nonetheless, flicker nest boxes attached near active flicker nest cavities did not alleviate starling nest-site competition. In fact, flickers lost nest cavities to starlings at a much higher rate (68%) than Ingold (1994) reported (14%) for this species in this area from 1990–1992. This disparity may be due in part to a difference in methodology between the studies. Previously, I (Ingold 1994) did not distinguish between flickers in the presence and absence of starlings, and may have observed a greater number of starling-free flickers in the earlier study. Further, nest boxes, which may have attracted additional starlings to flicker nest sites in this study, were not erected in the 1990–1992 study. Finally, flicker populations in the eastern United States have been declining during the past ten years (Moore 1995), while starling populations have been stable or increasing, particularly in the Great Lakes region (Cabe 1993). This trend, coupled with the possibility that suitable flicker nest substrates including snags and dead limbs are declining, could be resulting in fewer flicker nest cavities and greater starling/flicker nest-site competition.

Flickers, in the presence or absence of starlings, appeared to show little interest in nest boxes. Only 1 of 27 flickers pairs that lost nest cavities to starlings initiated a nest attempt in a nearby nest box. This may be explained in part by the fact that starlings often reacted aggressively toward flickers when they came too close to a usurped nest cavity. It may be that nest boxes, typically situated 1–2 m from a

flicker cavity, were within the territory that a starling defends when initiating a nest attempt. In addition, several starling pairs were often present at a cavity tree, and even after one starling pair usurped the flicker nest cavity, a second or third pair would often temporarily or permanently occupy the nest box, thus discouraging flickers from using the box. Bower (1995) reported that flickers nested successfully in the box he erected only after he shot several starlings that attempted to take over the box.

Only 1 of 14 flicker pairs in the absence of starlings opted to use a nest box rather than excavate a new nest cavity or renovate an old excavated cavity or knot hole. Although boxes were not erected until the flicker pair had initiated cavity excavation or renovation, flickers in the absence of starlings did not use them even after they had been in place for one or two years. This suggests that flickers had little inclination to use the boxes regardless of the availability of natural nest sites, or that in the absence of starlings (i.e., more densely forested areas), suitable nest trees or cavities may have been more common, and thus additional nest sites were unnecessary. Although flickers are not considered strong excavators (Bent 1939, Winkler et al. 1995), it appears that when given a choice, they prefer to excavate their own nest cavity in a snag or dead limb, or use a previously excavated or natural cavity than take up residency in a nest box. Bower (1995) and Jackson (1997) make several suggestions regarding the construction of nest boxes that might expedite their use by flickers. Bower (1995) suggests, however, that unless one is willing to control starlings and House Sparrows (*Passer domesticus*), it is unlikely that such boxes will attract flickers.

Although flickers generally avoided nesting in a box placed near their cavity or cavity start, the boxes in the absence of starlings did not appear to disturb them or deter them from carrying on their normal nesting activities. Eighty-six percent of starling-free flickers produced clutches and 64% eventually fledged young from cavities, even with a nest box situated nearby. Conversely, in the presence of starlings, with a single exception, nest boxes did not provide a suitable alternative nest site for flickers. However, aside from their common need to secure and defend a nest cavity, the ecological niches of starlings and flickers overlap relatively little. Once starlings in this study obtained a suitable nest cavity and initiated egg-laying, they generally ignored other cavity nesting species that took up residency in nearby cavities. Similarly, nesting flickers generally ignored nearby starlings once the latter had begun egg laying. Gutzwiller and Anderson (1986) and Ingold (1990) also reported that starlings and woodpeckers nested peacefully in proximity of each other after each pair had established control of their nest cavity and initiated egg laying.

Starling response to boxes.—Data in this study suggest that European Starlings prefer to usurp active flicker nest cavities, whether freshly excavated, previously excavated or knot-hole cavities, rather than undertake a nest attempt in a seemingly suitable nearby nest box. Only 7.5% of starlings chose to nest in a box rather than usurp an available flicker cavity or move to another location. In eight instances, starlings laid eggs in the nearby nest box rather than in the flicker cavity they usurped, and in four additional instances starling pairs initiated nest attempts in both the usurped flicker cavity and the nearby nest box. Although starlings are undoubtedly nest-site generalists that are willing to nest in cracks and crevices of buildings, old knot-hole cavities, old excavated cavities and nest boxes (Bent 1950, Zeleny 1969, Dakin 1984), data are accumulating that support the hypothesis that they prefer freshly excavated woodpecker cavities over many of the alternatives (see Ingold 1989, 1994; Kerpez and Smith 1990). However, an enigma remains. Although starlings usurped 42 active flicker nest cavities, they subsequently fledged young in only nine of them (21%). Of 32 woodpecker nest cavities usurped by starlings in east-central Ohio in 1990–1992, starlings subsequently abandoned 22 (69%) of them before initiating egg laying (Ingold 1994). Thus, although starlings seem to show a preference for freshly-excavated woodpecker cavities for nesting, they frequently fail to nest in the cavities they usurp. One possible explanation for this is that starlings sometimes drive away a woodpecker pair before it has completed excavating the nest cavity. I observed two nest cavities in this study and many in other studies that were taken over by starlings before completion. In

each of these instances, starlings abandoned the cavities probably because they were not deep enough. Nonetheless, there were several additional instances in this study and in past studies (Ingold 1989, 1994) in which I observed starlings usurp a completely excavated flicker nest cavity and then abandon it after building a partial or complete nest inside. It could be that excavating woodpeckers and/or the presence of freshly excavated cavities act as stimuli that activate aggressive starlings during the peak of their breeding season. Some starlings may be young and inexperienced nesters and simply fail to undertake a successful nest attempt in the usurped cavity. Clearly further research should be undertaken to address this "stimulus" hypothesis.

Implications for flicker reproduction.—Ingold (1994) suggested that although flicker pairs lost nest cavities to starlings, they may not have suffered reductions in their reproductive output, because these pairs often returned to their original cavity tree to nest successfully later in the season. Indeed the flicker nesting season may extend through July in Ohio, although the peak of their nesting effort occurs from early May through early June throughout most of their geographical range (Moore 1995). In this study, several flicker pairs in areas of starling overlap (at least 37%) that lost nest cavities to starlings in late April and early May, undertook a second nest effort in June or July, often in the same cavity tree or in another tree in the immediate area. However, the fecundity of late-nesting pairs was lower than that of starling-free pairs; moreover, when I arbitrarily divided all clutches into those completed before and after 1 June, the early nesters produced significantly more offspring. Ingold (1996) reports that early clutches, nestling numbers and fledgling numbers from flicker pairs studied from 1990–1992 and 1994–1995 in this area also were significantly larger than clutches, nestling numbers and fledgling numbers from late-nesting pairs. Thus, although flickers may routinely renest later in the season if their initial effort is disrupted (see Short 1982, Moore 1995, Winkler et al. 1995), they may still be at a reproductive disadvantage since their fecundity is reduced as the nesting season progresses. It is probable therefore, that flickers are subjected to opposing selection pressures. On the one hand, starling competition early in the season could select for delayed nesting; on the other hand, the detrimental effects of later nesting (i.e., warmer temperatures, less food and less time for the young to mature before winter) should select for early nesting (see Ingold 1996). The stronger of these selection pressures remains to be determined; even so, it is clear that European Starlings are having a significantly adverse effect on the reproductive success of Northern Flickers in Ohio.

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BREEDING BIOLOGY OF ACADIAN FLYCATCHERS IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—From 1993–1995, we located and monitored 601 Acadian Flycatcher (*Empidonax virescens*) nests in a large contiguous tract of bottomland hardwood forest on the White River National Wildlife Refuge, Arkansas. Annual reproductive success was significantly different among years; ranging from 10–25% (Mayfield estimate) over the three years of the study. There was no significant difference in nest success among study plots, with nesting success showing a trend of increasing late in the breeding season. Clutch size for nonparasitized nests averaged 2.9 ± 0.02 (SE) eggs with a mode of 3. Rates of Brown-headed Cowbird (*Molothrus ater*) parasitism were low (21%), accounting for 7% of all nest failures. However, parasitism by cowbirds resulted in a reduction of clutch size for nests initiated early (i.e., first nests and replacements) in the breeding season. Predation was the leading cause of nest failures, accounting for 75% of all failures. Snakes and avian predators were thought to be the leading cause of nest failures. Although additional factors must be investigated, preliminary results indicate that nest predation is a major influence on this population, despite the size of the forest tract. *Received 10 June 1997; accepted 27 Oct. 1997.*

Recent trends of many forest interior songbird populations have raised questions concerning the stability of these populations (Robbins et al. 1989, Askins et al. 1990, Terborgh 1992). As a result of the high degree of forest fragmentation and habitat loss in the eastern United States, factors on the breeding grounds have been suggested as the primary cause of migrant declines, presumably through decreased reproductive success (Martin 1992; Robinson et al. 1995a, b). In the southeastern United States, land conversion to agriculture and construction of levees have eliminated bottomland hardwood forest from much of the Mississippi Alluvial Valley (MAV; Pashley and Barrow 1992), which presumably has contributed to the decline of many forest interior songbird populations.

In this study, we initiated a demographic investigation of Acadian Flycatchers (*Empidonax virescens*) in an unfragmented bottomland hardwood forest in eastern Arkansas. The breeding biology of this species has been poorly documented, with the only detailed studies occurring on the northern periphery of its range (see Mumford 1964, Walkinshaw 1966). Here, we present an analysis of the breeding biology of Acadian Flycatchers in a large contiguous tract of bottomland hardwood forest in the Lower Mississippi Alluvial Valley. We also assess some of the factors likely to affect reproductive success.

STUDY AREA AND METHODS

Study area.—White River National Wildlife Refuge (NWR) is located in Phillips, Desha, Monroe, and Arkansas counties in eastern Arkansas, and appears as a long, narrow physiographic island in a highly fragmented landscape. Situated within the flood plain of the White River approximately 4–5 km above its confluence with the Mississippi River, the refuge consists almost entirely of bottomland hardwood forest. The 60,000 ha area is 4.8–16 km wide and extends approximately 104 river km along the White River. Of the total refuge acreage, 90% is forested, 9% is in waterways and lakes and 1% is in agriculture [U.S. Fish and Wildlife Service (USFWS) 1980].

Topography on the refuge is typical of naturally flooded bottomland forest, with wide flats broken by low ridges and swales. Bayous, oxbow-lakes, and sloughs are common throughout the refuge. Elevations range from 41–51 m above Mean Sea Level with 98% of the area falling below the 48-m contour (USFWS 1980). Flooding from the headwaters of the White River and backwaters of the Mississippi River annually inundates much of the refuge under the 45.7-m contour (J. Denman, pers. comm.). Except for the small acreage of upland hardwoods, the refuge is classified as palustrine, forested wetlands (Cowardin et al. 1979).

For this study, six rectangular 50-ha (500 m × 1000 m) plots were established within a single 1376 ha management compartment (Number 8) of contiguous homogenous habitat. The dominant overstory tree species on these plots were overcup oak (*Quercus lyrata*), Nuttall oak (*Quercus nuttallii*), green ash (*Fraxinus penn-*

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sylvanica), bitter pecan (*Carya aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), waterlocust (*Gleditsia aquatica*), sugarberry (*Celtis laevigata*), and cypress (*Taxodium distichum*). Understory vegetation was primarily seedlings and saplings of canopy trees (i.e., *Quercus* regeneration), plus possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorn (*Crataegus* spp.), and water elm (*Planera aquatica*). For additional information on the study area see Wilson (1997).

Nest monitoring.—Intensive nest searches were conducted on each plot throughout the breeding seasons of 1993–1995 to locate as many Acadian Flycatcher nests as possible (no plots were delineated in 1993 and nests were only located and monitored during June of 1993). Once a nest was located, its contents were noted. Poles with convex mirrors attached to one end were used to examine nests when contents could not be ascertained from the ground (Parker 1972). If nest height was too great for use of mirror poles (ca 8 m), the nest was observed from a distance using binoculars. Contents or stage of nesting was then determined by the behavior of adult birds (e.g., frequent visits by adults carrying food indicated the nest contained nestlings). Nest locations were then measured to the nearest grid point using a compass and a SONIN Combo Pro electronic distance estimator and recorded on a grid map to facilitate relocation. Nests were revisited every 3–4 days following Breeding Bird Inventory and Research Database (BBIRD) protocol (Martin et al. 1996) to determine the fate of each nest as accurately as possible.

Clutch size was based on the number of Acadian Flycatcher eggs over all nest checks. Nests that contained Brown-headed Cowbird (*Molothrus ater*) eggs may bias estimates of mean clutch size because it is possible that cowbirds removed eggs before the nest was found. Thus, estimates of clutch size are minimum estimates. Likewise, cowbird eggs and nestlings may disappear before nests are found, resulting in minimum estimates of brood parasitism.

Nesting success.—Nesting success was calculated by the methods of Mayfield (1961, 1975; see also Hensler and Nichols 1981), which estimate the probability of nest survival based on nest exposure days. A daily probability of nest survival (D) was calculated for each stage of the nesting period [i.e., egg stage (from first egg to first hatching) and the nestling stage (hatching to fledging)]. Nest-stage survival estimates (S) were obtained using the equation: $S = D^X$, where X is the number of days in the nest-stage. For Acadian Flycatchers, the egg stage was 15 days and the nestling stage was 14 days (see Results). Estimates of overall nesting success were obtained in the same manner. That is, the overall daily probability of nest survival was raised to the power of 29 (i.e., number of days in nesting period) to estimate the probability of nest survival (Hensler and Nichols 1981). Nests were excluded from analysis for any of three reasons: (1) the nest failed prior to laying of the first egg; (2) observers caused or influenced mortalities; and (3) the nest outcome was unknown. A nest was considered successful if it fledged at least 1 Acadian Flycatcher young. Conversely, a nest was considered a failure if its entire contents disappeared between checks and if insufficient time expired between checks for young to fledge, or if the only young to fledge were not Acadian Flycatchers.

Statistical analysis.—Tests of hypotheses comparing mean estimates of nest survival were conducted using the computer program CONTRAST (Hines and Sauer 1989, Sauer and Williams 1989) in the Microsoft-DOS operating system. Student's *t*-test and Analysis of Variance (ANOVA) were used to test for univariate differences in group means using PC-SAS (Vers. 6.11, SAS Institute 1992).

RESULTS

Nesting stages.—Females began building nests approximately 5–10 days after arrival with the majority of first nests constructed between 11 May and 22 May. Analysis of initial egg laying dates followed a bimodal distribution (Fig. 1), suggesting that Acadian Flycatchers produce more than one brood in the southern portion of their range. First eggs were laid on 19 May 1994 and 17 May 1995. One egg was laid per day, and incubation started with the penultimate egg. The mean incubation period was 14.3 days (standard error = 0.13, n = 73), and the mean nestling period was 13.6 ± 0.10 days (n = 58). Clutch size for all nonparasitized nests reaching the incubation period was 2.9 ± 0.02 eggs (n = 213; range = 2–4; mode = 3).

Parasitism and clutch size.—Brood-parasitism by Brown-headed Cowbirds averaged 21% during the study with only 8% of parasitized nests containing more than one cowbird egg (Table 1). However, brood-parasitism influenced clutch size of Acadian Flycatchers (t = 4.27, 100 df, $P < 0.001$) for all years combined. Parasitism had no significant effect on clutch size in 1993 (t = 0.481, 16 df, $P > 0.05$) and 1994 (t = 0.545, 60 df, $P > 0.05$), but clutch size was significantly lower in parasitized nests in 1995 (t = 4.56, 73 df, $P < 0.001$). Analysis of early and late nests (those initiated before or after 14 June; see Fig. 2) for all years showed that late-season nonparasitized clutches were significantly lower than early-season nonparasitized clutches (t = 2.29, 84 df, $P < 0.02$) and parasitized clutches were significantly lower than nonparasitized clutches during the early season (t = 5.05, 77 df, $P < 0.001$). Results of two-way ANOVA yielded a significant interaction between

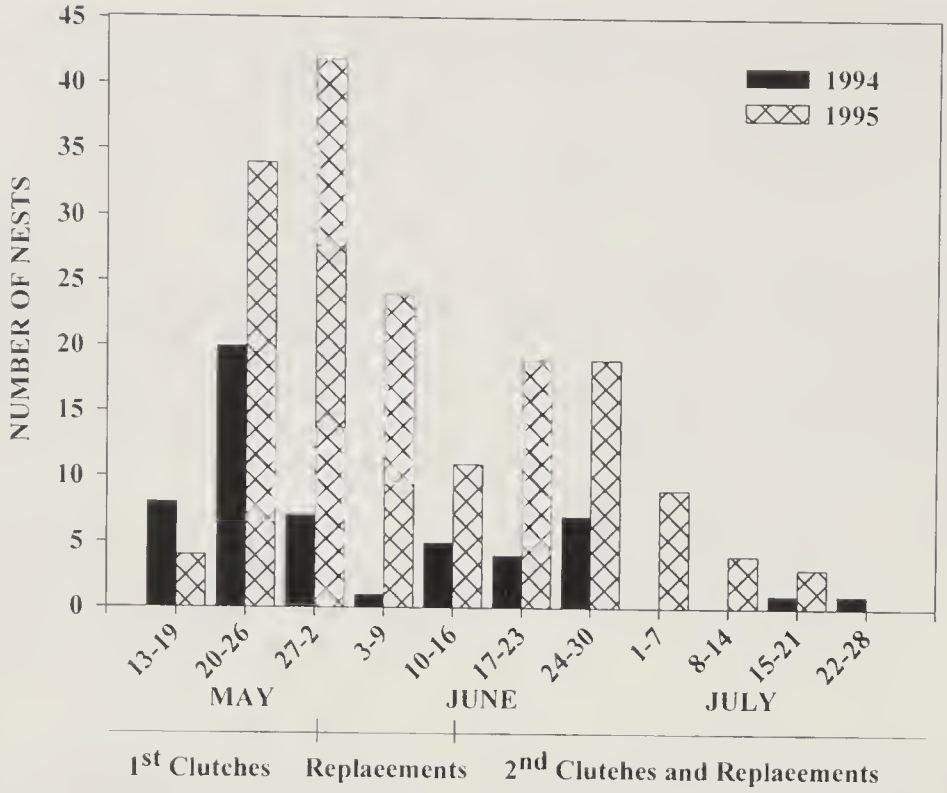

FIG. 1. Frequency distribution of initial egg laying dates for Acadian Flycatchers on White River NWR, 1994–1995.

clutch size of parasitized and nonparasitized nests across the breeding season [(i.e., first clutches, replacement clutches, and second clutches) F = 8.01, df = 5, 279, $P < 0.001$; Fig. 2].

Nesting success.—Acadian Flycatcher nesting success (probability of surviving the 29-day nesting period) on White River NWR varied throughout the study, ranging from 0.10 to 0.25 across all years of the study (Mayfield estimate, Table 2). Annual daily survival rates differed among years (χ^2 = 6.63, 2 df, P = 0.03) with daily survival rates being significantly lower in 1993 (χ^2 = 4.11, 1 df, P = 0.04). Daily survival rates for egg stage versus nestling stage were analyzed separately by plots within a year, among years and pooled over all years. No significant difference between egg stage and nestling stage rates of survival was found when the α-level was corrected using a Bonferroni adjustment (α = 0.008; Rice 1989). Analysis of early and late nests showed a significant difference in 1994 with late nests having a higher probability of survival than early nests (χ^2 = 5.50, 1 df, $P < 0.02$; Table 2). No significant differences were found between early and late nests in 1995 and because all nests in 1993 were considered early nests, no analysis was performed.

Nest failures were analyzed according to the causes of nest failure and the stage of nesting when failure occurred. The primary cause of nest failures in all years was predation, accounting for 75% of all failures (Table 3). Nest failure attributed to Brown-headed Cowbird parasitism was variable but low in all years, comprising 7% of all nest failures. Failures attributed to parasitism included nests that fledged at least one cowbird young, but no conspecific young, as well as nests that were abandoned after parasitism or the effects of parasitism [i.e., removal of host egg(s)]. Failures in which the entire contents of the nest disappeared between checks accounted

TABLE 1. Rates of Brown-headed Cowbird parasitism on Acadian Flycatchers, White River NWR, 1993–1995.

Year	Parasitism rates[a]	# Eggs[b] 1	# Eggs[b] 2
1993	13.5 (74)	12.2	1.3
1994	20.2 (129)	17.8	2.3
1995	22.6 (300)	21.3	1.3
1993–1995	20.7 (503)	19.1	1.6

[a] Percentage of Acadian Flycatcher nests parasitized (sample size).
[b] Percentage of total nests.

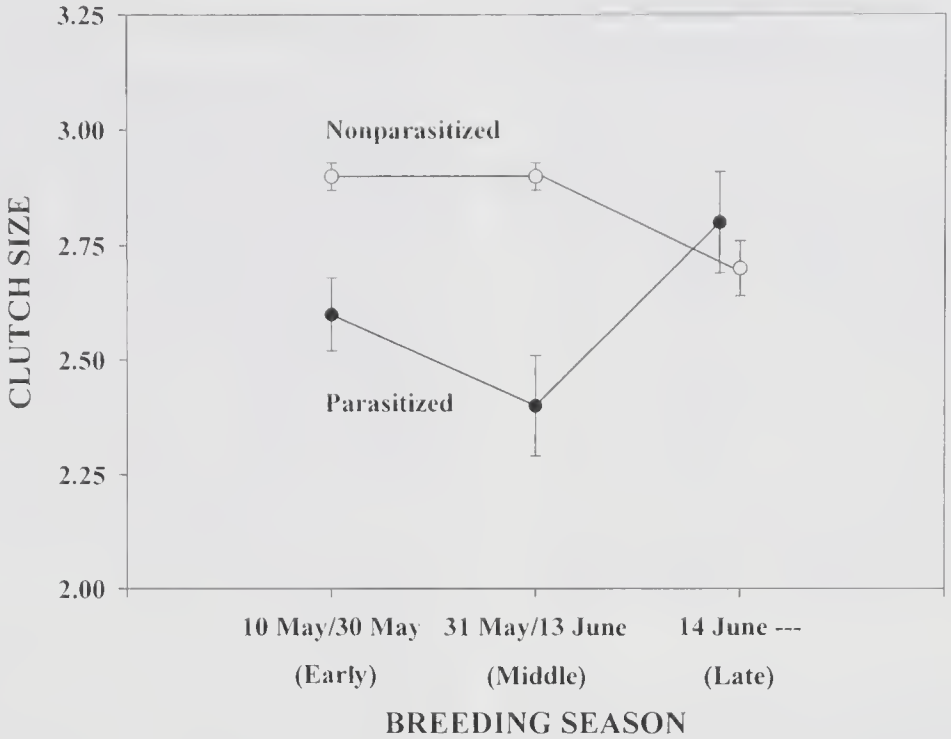

FIG. 2. Clutch size for parasitized and nonparasitized Acadian Flycatcher nests in three time periods within the breeding season on White River NWR, 1993–1995. ($F = 8.01$, df = 5, 279 $P < 0.001$; Error bars represent ± S.E.).

for 79% of all predation events, with the largest percentage of nest failures occurring in the egg stage across all types of failures.

DISCUSSION

Information on the nesting biology of the Acadian Flycatcher is scarce, with the previous detailed studies being from the northern periphery of the species' range in Michigan (Mumford 1964, Walkinshaw 1966). Thus, demographic analysis in different geographical regions is warranted. Our data represent the first demographic analyses of Acadian Flycatchers in the Lower Mississippi Alluvial Valley, and the total number of nests investigated (n = 601) was substantially larger than previous studies.

Nesting success.—Nesting success of Acadian Flycatchers on White River NWR varied from 10% to 25% annually (Mayfield estimate) over the three years of the study; the fraction of total nests fledging young varied from 16–30%. These estimates of nesting success are considerably lower than the 64.5%

TABLE 2. Mayfield estimates of nest survival for Acadian Flycatchers at White River NWR, 1993–1995.

	Mean nest survival rates[a]				
			Nesting period		
	Egg stage daily	Nestling stage daily	Daily	29 days[b]	Exposure days[c] (n)
1993	0.920 (0.016)	0.927 (0.024)	0.922 (0.013)	0.10	374.5 (37)
1994	0.953 (0.006)	0.930 (0.010)	0.945 (0.005)	0.18	1534 (128)
Early[d]	0.950 (0.007)	0.915 (0.014)	0.938 (0.007)	0.13	1127 (101)
Late[e]	0.966 (0.011)	0.964 (0.014)	0.965 (0.009)	0.36	407 (27)
1995	0.954 (0.004)	0.953 (0.005)	0.953 (0.003)	0.25	4040 (287)
Early	0.952 (0.005)	0.970 (0.004)	0.960 (0.003)	0.31	3290.5 (196)
Late	0.958 (0.007)	0.948 (0.009)	0.954 (0.005)	0.25	1258 (91)

[a] Mayfield estimates of mean daily nest success for the egg, nestling, and combined nesting period (± 1 SE).
[b] Nest survival for the combined egg (15 days) and nestling period (14 days).
[c] Exposure days are summed over the egg period (from first egg) and nestling period (number of nests).
[d] Nests initiated before 14 June.
[e] Nests initiated on or after 14 June.

TABLE 3. Summary of Acadian Flycatcher nests with known outcomes, White River NWR, 1993–1995.

	Fates[a] (%)			Failures (%)
	1993 (n = 42)	1994 (n = 129)	1995 (n = 306)	1993–1995 (n = 340)
Successful	16.6	29.5	30.0	—
Predation	66.6	56.6	50.6	75.3
Parasitism[b]	12.0	1.5	6.0	7.3
Abandoned	4.8	6.2	9.1	11.2
Weather	—	6.2	1.0	3.2
Inundation	—	—	2.3	2.0
Observer	—	—	1.0	1.0

[a] Excludes nests with unknown outcomes (1993, n = 50; 1994, n = 42; 1995, n = 32).

[b] Failures attributed to brood-parasitism include nests that fledged ≥1 cowbird young but no host young, as well as nests that were abandoned because of parasitism.

and 67.4% (fraction of nests fledging young) reported by Walkinshaw (1966) and Li (1994), respectively. However, Walkinshaw's data are 30 years old and may represent different degrees of forest fragmentation and environmental processes (e.g., nest predation and brood-parasitism) than today. Li (1994) evaluated the nesting success of several migratory bird species in the Ozark National Forest, a large contiguous tract of upland forest in northwestern Arkansas. In comparison, White River NWR, although large, is a long narrow fragment of bottomland forest surrounded by a large expanse of agriculture along the White River.

Estimates of nesting success for 1993 should be interpreted with caution since nests were only monitored during the month of June, reflecting events early in the breeding season. The large difference in estimates of nesting success between 1993 and 1994–1995 demonstrates the need for using caution when using partial data. That is, observed differences in nesting success may not be related to environmental factors but instead to experimental design (e.g., time period studied). For instance, late nests were more successful in 1994 and tended to be more successful in 1995 though not statistically.

Predation.—Nest predation on White River NWR was high, accounting for 75% of all known nest failures. Snakes and avian species were thought to be the leading predators of Acadian Flycatcher nests based on nest appearance at time of failure and anecdotal observations. Failures in which the entire contents of the nest disappeared between checks accounted for 79% of all nest failures. Gray rat snakes (*Elaphe obsoleta spiloides*) were observed depredating three Acadian Flycatcher nests and consumed the entire contents of the nest. Red-bellied Woodpeckers (*Melanerpes carolinus*) were also observed depredating Acadian Flycatcher nests on other bottomland sites in Tennessee (M. Marshall, pers. comm.) and Louisiana (K. Ouchley, pers. comm.), removing the entire nest contents. Barred Owls (*Strix varia*) present in high densities (pers. obs.) may have destroyed nests as suggested by Walkinshaw (1966).

Parasitism and clutch size.—Our data for nonparasitized nests are identical to reported clutch sizes for Acadian Flycatchers of 2.9 (range 2–4, mode = 3, Mumford 1964); 2.9 (range 2–3, mode = 3, Walkinshaw 1966); and 2.9 (Li 1994). Walkinshaw (1966) stated that in Michigan clutch size varied across the breeding season with first clutches being larger than second or replacement clutches. On White River NWR, clutch size also decreased from 2.9 ± 0.02 in early nests to 2.7 ± 0.06 in late season nests.

Cowbird parasitism was low (21% of all nests) compared with parasitism rates of other species in the midwestern United States (Robinson 1992; Robinson et al. 1995a, b), resulting in a small portion (7%) of all nest failures attributable to high rates of nest predation. Walkinshaw (1961) suggested that Acadian Flycatchers discontinue incubation of host eggs when cowbird eggs hatch first, resulting in failure of host eggs to hatch. However, Acadian Flycatchers are capable of producing a successful brood when host eggs hatch first. Of 104 parasitized Acadian Flycatcher nests, 2% were able to successfully produce conspecific young as well as a Brown-headed Cowbird young. In both cases, Acadian Flycatcher young hatched earlier than the cowbird young.

Brood-parasitism also influenced Acadian Flycatcher clutch size across the breeding season (i.e., early and late nests). Parasitized nests had smaller clutches for first nesting attempts and replacement clutches, presumably because cowbirds removed host eggs. However, parasitized nests had larger clutch sizes late in the breeding season, suggesting that

cowbirds are not removing host eggs late in the breeding season.

In summary, the population of Acadian Flycatchers in this study appears to be influenced primarily by high rates of nest predation, for brood-parasitism by Brown-headed Cowbirds contributed only a small amount to overall nest failure. However, both factors influenced early nesting attempts more than late nesting attempts. It is not known if birds fledging late in the breeding season have a decreased probability of survival compared with early fledges, but this factor certainly has the potential to influence population dynamics. Other factors that could play critical roles in population dynamics of Acadian Flycatchers in bottomland forests include number of renesting attempts and broods, food abundance, and loss of appropriate habitat features. Consequently, future research with color-banded individuals should focus more on productivity (number of young per pair per year), annual survival of adult and juveniles, and habitat features that influence these parameters.

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COMPARATIVE REPRODUCTIVE BIOLOGY OF THREE SPECIES OF SWALLOWS IN A COMMON ENVIRONMENT

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ABSTRACT.—We compared the breeding biology of sympatric and contemporaneously breeding populations of Tree (*Tachycineta bicolor*), Barn (*Hirundo rustica*) and Cliff swallows (*Petrochelidon pyrrhonota*) in 1994 and 1995 in central New York to characterize their life histories under common environmental conditions. Laying dates did not vary among species, but average clutch sizes were largest in Tree Swallows (5.7 eggs), intermediate in Barn Swallows (4.7 eggs) and smallest in Cliff Swallows (3.5 eggs). Two broods were common in Barn Swallows, but Tree Swallows raised only one, and we suspect that Cliff Swallows raised only a single brood. Relative egg mass (egg mass/female mass) was higher in Barn than in Tree swallows. Most nests fledged young, and fledging success did not vary among species. Growth rates of four nestling traits were measured (mass, wing chord, tarsus and bill), and overall, Tree Swallows grew the fastest. Peak nestling mass was substantially higher in Cliff Swallows than the other species, probably because they gained the most fat. A literature survey of hirundinid growth rates also suggested that Tree Swallows grew faster than the other species. Per capita provisioning rates of parents (trips/nestling/h) increased seasonally and were highest in Barn Swallows. Slower growth despite high feeding rates suggests either lower feeding efficiency or more severe effects of ectoparasitism in Barn Swallows compared to the other species. Our results show that clutch size, number of broods/season and the pattern of nestling growth vary among species and probably represent differences that have evolved because of differences in (1) the availability of suitable nest sites (i.e., the limited breeding opportunities hypothesis), (2) food supply, or (3) demographic trade-offs. *Received 25 July 1997, accepted 11 Nov. 1997.*

Theoretical and empirical studies suggest that food supply (Lack 1968, O'Connor 1978), nest predation (Lima 1987, Martin 1995) and probability of adult survival (Saether 1988, Martin 1995) account for much of the interspecific variability that exists in reproductive traits such as clutch size, number of broods per season, and patterns of nestling growth. Much information has come from literature- or museum-based comparative studies (e.g., Ricklefs 1968, Kulesza 1990, Martin 1995), with the most revealing comparisons being of closely related and ecologically similar species that differ substantially in one or more reproductive traits (e.g., Murphy and Fleischer 1986, Martin 1988, Murphy 1989, Ricklefs 1997). A question that arises in such studies, however, is whether the presumed species level features are genetically fixed traits or represent phenotypic responses to environmental factors. Intraspecific comparisons have often shown that traits such as timing of breeding, clutch size, egg mass and even length of incubation vary with environmental conditions (e.g., Murphy 1983, 1986; Hussell and Quinney 1987; Brawn 1991). Thus, contemporaneous studies of sympatric, related and ecologically similar species are particularly useful for characterizing reproductive patterns and identifying the ecological basis for life history differences (e.g., Turner 1982, Ekman and Askenmo 1986, Murphy 1988).

Swallows (family Hirundinidae) are a large, monophyletic group of species (Sheldon and Winkler 1993) that are all narrowly adapted to the capture of aerial insects. Many nest colonially (Shields et al. 1988) and most species nest either in abandoned cavities in trees or earthen banks, or build protected mud nests, and all temperate-zone species are migratory. Seven of the eight species that breed in North America are widely distributed (A.O.U. 1983), and despite the fact that four or five species may breed in close proximity to one another in eastern North America, Samuel (1971) published the only comparison of reproduction in sympatric populations of North American breeding hirundinids. Swallows appear to differ substantially in clutch size and possibly other traits, but given that clutch size (Hussell and Quinney 1987) and nestling growth rates (Quinney et al. 1986) of Tree

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Swallows (*Tachycineta bicolor*) vary with food abundance even over short distances, interspecific differences in clutch size and other reproductive traits of swallows in large part may be due to environmental factors and not genotypic differences. We therefore compared the breeding biology of Tree, Barn (*Hirundo rustica*) and Cliff swallow (*Petrocheldon pyrrhonota*) populations that bred in close proximity to one another to determine if previously documented differences in clutch size (Shields and Crook 1987, Robertson et al. 1992, Brown and Brown 1995) existed in sympatric populations. We also used additional information on nestling growth patterns and parental feeding rates to attempt to evaluate whether variability in swallow life histories is related primarily to characteristics of food supplies, differences in adult mortality, nest site limitation, or energetic constraints.

METHODS

Our study was conducted in 1994 and 1995 at two sites in Delaware County, NY. The main study area was located in abandoned pastures that ran along Charlotte Creek about 4.5 km east of Davenport, NY (42° 27′ N, 74° 47′ W). We established two nest box grids (15 and 16 boxes) on either side of the creek in July 1993. The grids were separated by about 100 m of stream and open field, and both were located less than 400 m from a barn that supported Barn and Cliff swallows. The second site, located 8 km away and also along Charlotte Creek, supplemented our observations from the primary site. Only Tree and Barn swallows bred at site two. We combined data from the sites because we found no differences in breeding date, clutch size, egg mass or nestling growth when comparisons were made within species.

Tree Swallow nests were visited every 2–3 days in the early breeding season to establish egg laying dates and clutch size. Breeding date was the first day of egg-laying and it was counted continuously from 1 May (e.g., 1 June = day 32). Clutch size was the number of eggs found after successive visits showed no change in the number of eggs in the nest. All eggs were marked at the blunt end with a pencil, and maximum egg length and breadth were measured with dial calipers. Unincubated eggs were weighed to the nearest 0.1 g using a 10 g Pesola scale. Fresh egg mass was estimated for other eggs using length and breadth measurements (e.g., Murphy 1983). We made daily visits around the expected hatching date to determine hatching success and initial brood size, and then visited nests every 2–3 days during the nestling period to measure changes in nestling mass (0.1 g using either a 10 or 50 g Pesola scale), and growth of the tarsometatarsus (=tarsus), bill (anterior edge of nares to bill tip) and wing chord [all linear measurements made to the nearest 0.05 mm using dial calipers with the exception of wind chord (nearest 0.5 mm with wing ruler)]. We followed the same procedures with Barn and Cliff swallows, but because they nested at less accessible locations (mainly Cliff Swallows) we obtained fewer data and more time elapsed between nest checks (2–5 days). We often had to remove a portion of the neck of the gourd-shaped mud nest of the Cliff Swallow to gain access. Parents repaired the damage, but for this reason also we visited their nests less frequently. Most Barn Swallow nests were located on the tops of beams inside the two barns. Cliff Swallows attached their nests directly to the outside wall of the barn. To prevent the accidental loss of Cliff Swallow nests when we removed eggs and/or nestlings, in 1995 we reinforced many of the nests by stapling a sheet of fiberglas screening over the nest to the eaves of the barn.

In lieu of measuring food supply, in 1995 we made one hour observations of the rate of parental feeding visits to nests to measure foraging efficiency. All three species feed their young a bolus of small insects that have been captured from the air, and in making the comparison of feeding rate we assume that all parents attempted to feed their young with equal vigor and that one nestling was fed per visit (Turner 1982, Brown and Brown 1995). A small hill that overlooked the Tree Swallow colony allowed simultaneous observations of several nests. We could also observe Tree and Barn swallow nests simultaneously at site 2. In all cases, we made observations between 08:00 and 12:00 EST (none during poor weather).

We used the STATISTIX (version 4.1, Siegel 1992) and the general linear models procedure of SAS (SAS 1992) to test for annual and interspecific differences in reproduction and nestling growth. Standard parametric statistics (analysis of variance, *t*-tests, least squares linear regression) were used to compare breeding date, clutch and egg size among species and years. Equivalent nonparametric statistics were used when variances were heteroscedastic. Nestling growth rates were computed using least squares linear regression during the period of linear growth. This corresponded to days 3–10 (hatching = 1) for mass, day 5 onward for wing chord, days 1–10 for tarsus and days 3–14 for bill. Each nest was treated as a single observation; hence, the statistics (mean, SD, *n*) given below always reflect the number of nests from which data were collected. We also described changes in nestling mass with age by calculating growth rates using Ricklefs' (1967) graphical method. Unless otherwise stated, statistical significance was established at $P \leq 0.05$. All statistical analyses were performed with SAS (ver. 6.12) on a DEC Alpha 2100A/250 under OpenVMS.

RESULTS

Breeding statistics.—Tree Swallows initiated clutches significantly earlier in 1995 than in 1994 ($t = 5.62$, $P < 0.001$), and although Barn Swallows showed the same trend, annual

TABLE 1. Reproductive statistics for sympatric populations of Tree, Barn and Cliff swallows breeding in Delaware Co., NY, during the 1994 and 1995 breeding seasons.

Species	Year	Laying date[a] $\bar{x}$ (SD; n)	Clutch size $\bar{x}$ (SD; n)	Egg mass (g) $\bar{x}$ (SD; n)
Tree Swallow	1994	25.0 (6.60; 14)	5.8 (0.70; 14)	1.85 (0.158; 14)
	1995	14.2 (3.63; 24)	5.7 (0.74; 25)	1.85 (0.141; 23)
Barn Swallow	1994	26.6 (11.07; 11)	4.5 (0.97; 13)	1.90 (0.128; 9)
	1995	19.4 (8.44; 10)	5.1 (0.57; 10)	1.86 (0.130; 8)
Cliff Swallow	1994	31.0 (6.20; 5)	3.3 (1.21; 6)	2.19 (0.097; 5)
	1995[b]	65.2 (3.06; 6)	3.7 (1.03; 6)	2.15 (0.147; 6)
Two-way ANOVA		F (P)	F (P)	F (P)
Species		1.58 (>0.05)	40.76 (<0.001)	24.06 (<0.001)
Year		12.36 (0.001)	0.12 (>0.05)	0.14 (>0.05)
Species × year		0.47 (>0.05)	0.31 (>0.05)	0.22 (>0.05)

[a] Dates counted consecutively with day 1 = 1 May.
[b] 1995 Cliff Swallow statistics refer to late breeding attempts.

differences were not significant (Table 1; t = 1.67, $P > 0.05$). Cliff Swallows laid eggs during the period of first clutches in 1994, but did not lay again at our site until Barn Swallows initiated second clutches in 1995 (Table 1). Results of a two-way analysis of variance (ANOVA) with year and species as main effects indicated that only the effect of year was significant (Table 1). Tree Swallows raised one and most Barn Swallows raised two broods. Second clutches of Barn Swallows were laid an average of 39 days after the start of first clutches in 1995, and at the same time as Cliff Swallows (t = 1.09, df = 11, $P >$ 0.05). In both years Cliff Swallows appeared to raise only a single brood.

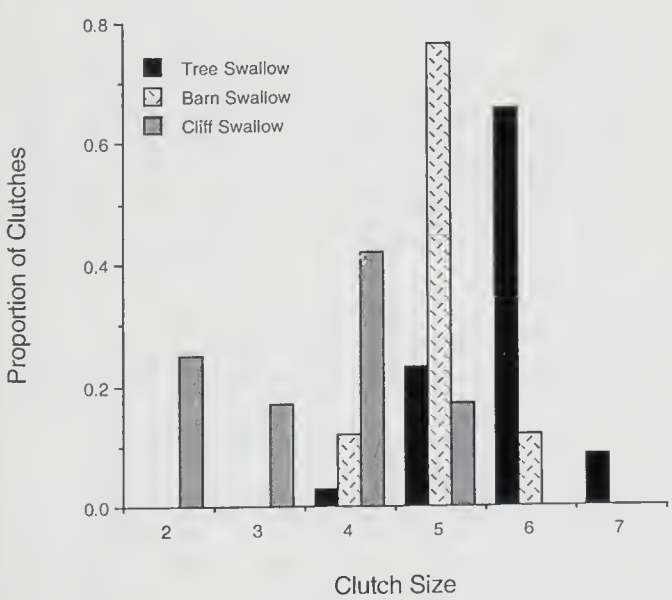

FIG. 1. Comparison of clutch sizes of Tree, Barn and Cliff swallows breeding in Delaware County, NY, in 1994 and 1995.

Modal clutch size of Tree Swallows was six eggs ($\bar{x}$ = 5.7, SD = 0.72, n = 39). Barn Swallows usually laid five eggs in first clutches ($\bar{x}$ = 4.7, SD = 0.86, n = 23), while 3–4 eggs were typical of Cliff Swallows ($\bar{x}$ = 3.5, SD = 1.09, n = 12; Fig. 1). A two-way ANOVA (species and year) showed that the species effect was significant, but that year and species × year interaction were not (Table 1). Clutch size declined with date when all three species were combined (r = 0.405, df = 55, $P < 0.002$). Slight differences in date might have contributed to the clutch size differences, but after removing date effects the species differences persisted (F = 13.64, df = 2, 54, $P < 0.001$). Residual clutch size was 0.6 and 1.6 eggs larger in Tree Swallows than Barn and Cliff swallows, respectively (Tukey's test: $P < 0.05$). Barn Swallows laid more eggs in first than in second nests ($\bar{x}$ = 4.0, SD = 0.19, n = 8; t = 2.26, P = 0.03).

Egg mass did not differ among years but Tree and Barn swallows produced significantly smaller eggs than Cliff Swallows (Table 1). Cliff Swallows (23.4 g; Brown and Brown 1995) are heavier than Barn (19.6 g; R. Montgomery, pers. comm.) and Tree swallows (21.1 g; Robertson et al. 1992), which possibly explains the larger Cliff Swallow eggs. We thus compared relative egg mass [arcsine(egg mass/adult mass)] and found that Barn Swallows laid relatively larger eggs (0.097) than Tree Swallows (0.088), but Cliff Swallows (0.093) did not differ from either species (F = 16.62, df = 2, 69, $P < 0.001$; *a posteriori* comparisons made using Tukey's test).

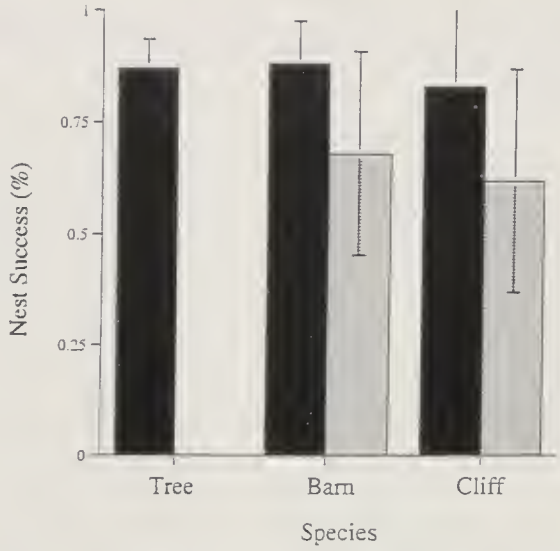

FIG. 2. Fledging success (nestlings fledged/egg laid) for Tree, Barn and Cliff swallows breeding during 1994 and 1995 in Delaware Co., NY. Black bars refer to early (or first) nests of the season and shaded bars represent late (or second) nests. The vertical lines indicate ±2 standard errors.

No nests were lost to predation, and most losses resulted from the starvation of 1 or 2 nestlings within a nest. Regardless of species, about 85% of young fledged from broods that were raised during June (Fig. 2; $F = 0.11$, df = 2, 54, $P > 0.05$). Second broods of Barn Swallows and the late 1995 Cliff Swallow nests tended towards lower success than that of the early broods (Fig. 2), but the difference was not significant in either Barn ($t = 1.95$, df = 22, $P > 0.05$) or Cliff swallows ($t = 1.39$, df = 9, $P > 0.05$).

Nestling growth.—The rate at which nestlings gained mass did not differ between years in Tree ($t = 0.96$, df = 18 broods, $P > 0.05$), Barn ($t = 1.44$, df = 21, $P > 0.05$) or Cliff swallows ($t = 0.12$, df = 9, $P > 0.05$). Likewise, first and second broods of Barn Swallows grew at virtually identical rates in 1995 ($t = 0.63$, df = 15, $P > 0.05$). Analysis of wing chord growth yielded identical results. Slight annual differences were found for tarsus and bill growth of Tree Swallows, but because the differences were small compared to interspecific variation, we combined all data between years before comparing species.

Growth rates of all four traits differed significantly among species (Table 2). Cliff Swallows gained mass 13% faster than Barn Swallows, and although Tree Swallows were closer to Cliff Swallows, their growth rate did not differ from either species (Tukey's test: $P > 0.05$). The peak mass of Cliff Swallows was 21% and 31% higher than that of Tree and Barn swallows, respectively (Fig. 3, Table 2), and the 8% higher peak mass of Tree Swallows compared to Barn Swallows was also significant (Tukey test: $P < 0.05$). Differences in the rate of wing chord growth were not large, but the wing chords of Tree Swallows grew faster than those of Cliff Swallows (Table 2). On the other hand, the tarsae of Cliff Swallows grew the fastest and Barn Swallows the slowest (Table 2). Tree Swallows did not differ from either species. Finally, growth of the bill was slower in Cliff than in both Barn and Tree swallows (Table 2).

Feeding rates.—Per capita provisioning rates to first broods of Tree and Barn swallows increased with nestling age ($r = 0.543$) and date (late May through mid June; $r = 0.674$, df = 39, $P < 0.001$ for both). We therefore included both variables and both species in a multiple regression analysis of per capita feeding rate. All three variables contributed significantly to the model (t-test on type III sums of squares: date, $P < 0.001$; nestling age, $P = 0.001$; species, $P < 0.001$; model $R^2 = 0.783$, df = 3, 37, $P < 0.001$). After con-

TABLE 2. Summary statistics describing nestling growth rates for Tree, Barn and Cliff swallows breeding in Delaware Co., NY, during the 1994 and 1995 breeding seasons. Species sharing the same letter do not differ significantly from one another (n = number of nests).

Variable	Tree Swallow $\bar{x}$ (SD; n)	Barn Swallow $\bar{x}$ (SD; n)	Cliff Swallow $\bar{x}$ (SD; n)	Statistic F or H (P)[a]
Mass gain (g/d)	2.14 (0.29; 20)AB	1.96 (0.29; 23)B	2.21 (0.32; 11)A	3.45 (0.039)
Peak mass (g)	23.3 (1.22; 32)B	21.6 (1.47; 20)C	28.3 (1.84; 11)A	80.03 (<0.001)
Wing growth (mm/d)	5.49 (0.20, 19)A	5.35 (0.44; 22)AB	5.15 (0.44; 12)B	6.06 (0.048)
Tarsus growth (mm/d)	0.96 (0.10; 22)AB	0.84 (0.16; 21)B	1.08 (0.38; 8)A	9.97 (0.007)
Bill growth (mm/d)	0.25 (0.04; 20)A	0.25 (0.04; 23)A	0.21 (0.04; 11)B	4.13 (0.02)

[a] F and H refer to results of analysis of variance and Krusakal-Wallis tests, respectively.

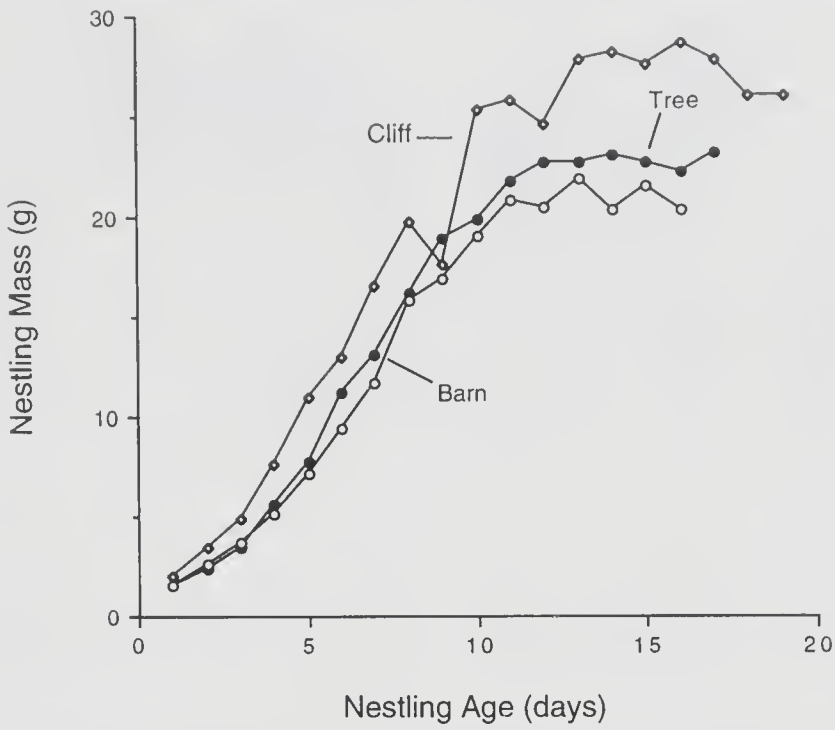

FIG. 3. Increase in mass of nestling Tree (●), Barn (○) and Cliff swallows (◇) from populations that bred sympatrically in Delaware Co., NY, in 1994 and 1995.

trolling for the effects of date and age, residual feeding rate of Barn Swallows ($\bar{x}$ = 0.9 trips/nestling, SD = 2.00, n = 14) was higher than that of Tree Swallows ($\bar{x}$ = −0.5, SD = 0.99, n = 27; $t_{\text{unequal variance}}$ = 2.46, P = 0.025). Per capita feeding rates to late Barn and Cliff swallow broods varied with brood size (r = −0.664, df = 19, P = 0.001). After removing the effect of brood size, Barn Swallow residual feeding rate ($\bar{x}$ = 0.7 trips/nestling, SD = 1.19, n = 11) was slightly but not significantly higher than that of Cliff Swallows (−0.8, SD = 3.58, n = 10; $t_{\text{unequal variance}}$ = 1.24, $P > 0.05$). Residual per capita feeding rate to first (−0.1 trips, SD = 2.66) and second (0.2 trips, SD = 1.66) Barn Swallow broods did not differ (t = 0.35, $P > 0.05$) after accounting for the negative correlation of per capita feeding rate with brood size.

DISCUSSION

Our description of interspecific differences in clutch size and number of broods per season are consistent with previously published reports in showing that Tree Swallows lay the largest clutches and produce only a single brood per year (Robertson et al. 1992). The Barn and Cliff swallows also differed significantly in clutch size (Samuel 1971, Grant and Quay 1977, Shields and Crook 1987, Brown and Brown 1996, this study) and in number of broods per season (often 2 in *H. rustica*, and 1 in *P. pyrrhonota*; Shields and Crook 1987, Brown and Brown 1995). On the other hand, when all three species were present neither breeding date nor fledging success differed among them. The larger Tree Swallow clutches in part might be related to the use of nest boxes with a large internal space (Robertson and Rendell 1990), but we doubt that this is the principal explanation for the interspecific differences since in our population we have found no relationship between clutch size and cavity floor area despite large variation in the latter variable (M. T. Murphy, unpubl. data). Goodman (1982) also reported that clutch size was independent of nest cup volume in Barn Swallows. Given the similarity in timing of breeding, proximity to one another, and exposure to identical climatic conditions, the interspecific differences in clutch size and number of broods most likely represent evolved differences rather than proximate responses to weather or food supply (e.g., Hussell and Quinney 1987).

Although less dramatic, rates and patterns of nestling growth also differed. Based on absolute growth rate (Table 2), nestling Tree Swallows grew either the fastest (wing chord) or equalled the most rapidly growing species

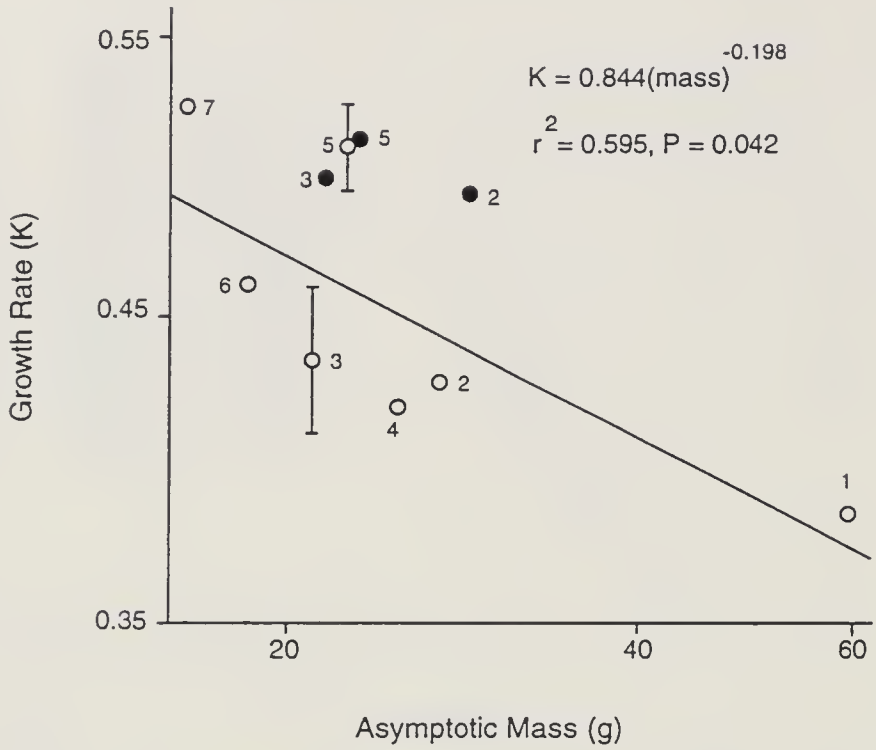

FIG. 4. The relationship between nestling growth rate (K of Ricklefs 1967) and asymptotic mass for swallows breeding in north temperate latitudes. Open circles represent literature data (see Appendix). Filled circles are for the Tree, Barn and Cliff swallow populations in this study. Numbers refer to species: 1 = *Progne subis*; 2 = *Petrochelidon pyrrhonota*; 3 = *Hirundo rustica*; 4 = *Delichon urbica*; 5 = *Tachycineta bicolor*; 6 = *Stelgidopteryx serripennis*; 7 = R*iparia riparia*. Vertical bars for *H. rustica* and *T. bicolor* are ±2 standard errors around the mean (n = 3 and 4, respectively), and do not include data reported here. Likewise, the power equation relating growth rate to mass does not include our data, but is based on the mean for the seven species shown [*T. thalassina* was not included (see Appendix) because growth data were derived from a single brood].

for mass, tarsus and bill. Mass and tarsus growth were slower in Barn Swallow nestlings than the other species, and Cliff Swallow nestlings exhibited the slowest wing chord and bill growth rates. Nestlings of all three species exceeded adult mass (as is typical of hirundinids), but Cliff Swallows in particular were very heavy compared to the other species. Cliff Swallows remain in the nest for about 24 days (Samuel 1971, Brown and Brown 1995), Barn Swallows usually fledge at 21 days (Shields and Crook 1987), but Tree Swallows take only 18–22 days (Robertson et al. 1992). The shorter nestling period of Tree Swallows follows from their rapid growth, while the long nestling period of Cliff Swallows is probably related to their slow wing growth and relatively large mass.

Differences in adult size confound comparisons of growth rate because growth rate and size tend to be negatively related (Ricklefs 1968). To provide a basis for evaluating our results, we compared growth rate (K; Ricklefs 1967) for our three populations, and for other populations and species of temperate-zone breeding swallows (Appendix). Our estimate of Tree Swallow growth rate (K = 0.510) was slightly faster than sympatric Barn (K = 0.496) and Cliff swallows (K = 0.490). Among the sample of seven species of temperate zone breeding swallows with data, growth rate declined significantly with asymptotic nestling mass (Fig. 4). We used this relationship to predict expected growth rates for all populations (based on asymptotic mass). Comparisons of residual growth rates (observed rate − predicted rate) showed that Tree Swallows (0.04, SD = 0.014, n = 5 studies) grew faster ($t_{\text{unequal variances}}$ = 3.31, P = 0.03) than Barn Swallows (−0.02, SD = 0.035, n = 4 studies) when the effect of body size was removed. Clearly, it is impossible to fully characterize nestling growth in any species without examining spatial and temporal variability, but given the available data, we conclude that Tree Swallows grow relatively rapidly and that Cliff Swallows gain relatively more mass (probably fat) prior to fledging than other swallows.

Interspecific differences in clutch size.—We

are unaware of any attempts to explain why the life histories of these species differ to such a degree. Taxonomic affiliation seems unlikely since differences in clutch size can be large even among congeners [e.g., clutch sizes of Violet-green (*T. thalassina*) and Tree swallow differ significantly; Brown et al. 1992 and Robertson et al. 1992], and other traits, such as coloniality, are not constrained by phylogeny (Shields et al. 1988). Nest predation has probably not been a major force shaping their differences because so few nests are lost to predators (Shields et al. 1988). Moreover, trends within swallows are opposite of the theoretical predictions. Large clutch size is generally associated with low nest predation rates (Martin 1995), yet Tree Swallows lay the largest clutches and under natural conditions probably lose more nests to predators than either of the other species (Shields et al. 1988, Rendell and Robertson 1989). We suggest the following as plausible explanations for the differences in clutch size, and possibly other traits: (1) foraging behavior and food supply; (2) demographic adjustments to adult mortality; (3) energetic costs of nest construction; and (4) nest site limitation.

Although these species are highly adapted to aerial insectivory, and thus susceptible to sudden and sometimes drastic declines in food supplies as a result of poor weather (Bryant 1973, Turner 1982, Brown and Brown 1995), their foraging behaviors differ. Cliff Swallows tend to forage at heights of 50 m or more above ground (Brown and Brown 1995) but Barn and Tree swallows generally forage much lower, often just above the surface of fields and streams (Samuel 1971, pers. observ.). Variability in aerial insect abundance increases with altitude (Lack 1968, Bryant 1973), and Brown (1986) has shown that Cliff Swallows exhibit behaviors indicating that they use highly variable food supplies. Albeit limited, our observations indicate that Cliff Swallows had the most variable feeding rates. Theory predicts a reduction in clutch size when food supplies vary unpredictably and to the point that the risk of failure caused by the complete starvation of large broods is high (Murphy 1968). Thus, the small clutches of Cliff Swallows may represent an adaptation to the use of highly variable food supplies. The high provisioning rates of Barn Swallow (but which did not support higher growth rates) also suggests that Tree and Barn swallows either forage in different strata or habitats, or that they capture different prey (e.g., Turner 1982).

Demographic trade-offs between reproduction and adult survival can be driven by either extrinsic mortality (e.g., storms, predators) or costs of reproduction (Williams 1966, Charnov and Krebs 1974), but in either case high adult mortality favors early breeding and high fecundity (Law 1979, Reznick et al. 1990, Stearns 1992). There is little to no evidence for the existence of reproductive trade-offs in swallows (DeSteven 1980, Bryant 1979, Wheelwright et al. 1991), but annual survivorship does appear to differ among these species, possibly from events in the nonbreeding season. Brown and Brown (1995) used Jolly-Seber stochastic models to show that 57% of Cliff Swallow adults survived between breeding seasons. Barn and Tree swallow survivorship has not been estimated with the same methods, but survivorship estimates based on Farner's (1955) approach are higher for Cliff Swallows (48%) than for both Barn (42%) and Tree (40%) swallows (data from Martin 1995). The small clutch size of Cliff Swallows is thus consistent with their relatively higher survivorship.

Tree Swallows differ from the other species in that they nest in abandoned tree cavities, and individuals failing to secure a cavity do not breed. Although Barn and Cliff swallows build their own nests, and most birds probably secure a mate and breed, natural sites suitable for the placement of Barn Swallow nests may be limited (Speich et al. 1985). On the other hand, Brown and Brown (1995) stated that there was no evidence for a shortage of either colony or nest sites for Cliff Swallows. The nest site limitation hypothesis predicts that females should invest heavily in reproduction when breeding opportunities are limited (Martin 1993, Beissinger 1996), and in accordance, clutch sizes of these three species are directly correlated with nest site shortage. Moreover, other predictions (see Beissinger 1996) of the limited breeding opportunities hypothesis lend qualitative support. Intraspecific nest takeover and infanticide occur among Tree Swallows (Robertson 1990), and Tree Swallows lose nests to larger secondary cavity nesters (Rob-

ertson and Rendell 1990). Shields and Crook (1987) found evidence of infanticide in Barn Swallows and attributed it to competition for limited nesting sites. Additional predictions of the limited breeding opportunities hypothesis for which data are lacking are that the proportion of nonbreeding individuals and average age of first reproduction should be highest in Tree Swallows (see Beissinger 1996).

The energetic costs of nest construction probably also vary among swallows in a way that could account for the differences in clutch size. Nest building in Tree Swallows entails only the collection of twigs and feathers to line their cavity nest. Barn and Cliff swallows, on the other hand, carry considerable amounts of mud to build a complicated nest. Shields and coworkers (1988) estimated that a new Barn Swallow nest required between 1000 and 2000 mud gathering trips. Cliff Swallow nests are larger; they are attached directly to the vertical face of a surface, and probably require even more mud gathering trips than Barn Swallows. A trade-off may exist between clutch size and the energetic cost of nest construction. In fact, Brown and Brown (1996) reported that clutch size declined significantly with increasing nest size in Cliff Swallows. On the other hand, Barn Swallows that reused nests (and therefore avoided the heavy cost of nest construction) had the same seasonal egg production as females with new nests (Shields et al. 1988).

At present we cannot unequivocally exclude any of the hypotheses that we have proposed to explain the differences in clutch size and annual fecundity of Tree, Barn and Cliff swallows. Considerable evidence supports the nest site limitation hypothesis. In addition, the apparent differences in annual survival that are consistent with the demographic trade-off hypothesis might arise from selection for higher reproductive effort by the nest site limited species. However, differences in nestling growth exist that are also consistent with the food supply hypotheses. For instance, Tree Swallows grew faster than Barn Swallows despite lower feeding rates. Tree Swallows thus appear capable of providing more food per unit effort than Barn Swallows, which may indicate that they exploit a more abundant and/or more stable food supply. Two other explanations for the seemingly more efficient growth of Tree Swallows are that (1) they experience less severe ectoparasite infestations than the other species (Shields and Crook 1987, Brown 1988), and (2) poor nestling Barn Swallow growth might stem from a poorly insulated nest. Barn Swallow nests are very open and exposed compared to the cavity nests of Tree Swallows, and nestling Barn Swallows may use more energy thermoregulating than do nestling Tree Swallows.

Differences in peak nestling mass also suggest that food supplies differ among these species. Nestling birds use fat as insurance against temporary food shortages (Lack 1968, Bryant and Hails 1983), and nestling fat content and variability in insect abundance increase with average adult foraging height in aerial insectivores (Bryant and Hails 1983). Cliff Swallows forage higher than the other species, lay the smallest clutches, have the most variable feeding rates, their nestlings grow relatively slowly (yet attain the greatest peak mass) and remain in the nest longer than Tree and Barn Swallows. These patterns all suggest that Cliff Swallows experience high stochastic variation in food supplies. Barn Swallows are perhaps the most perplexing in that nestling growth is not rapid, despite the fact that they alone regularly raise two broods. Perhaps historical differences in geographic distribution and length of the breeding season (more southern and longer in the Barn Swallow) favored multiple broods that grow at moderate rates. Without the option of second broods and potential intraseasonal costs of reproduction (McGillivray 1983, Smith et al. 1987), larger clutches and rapid growth would have been more likely to evolve in Tree Swallows.

We do not purport to have explained why clutch size, number of broods and growth rates differ among these species. However, our data strongly point to the need to test additional predictions of the limited breeding opportunities (Beissigner 1996) and measure for differences in the abundance and variability of food supplies. In addition, comparative studies of survivorship in sympatric populations of three or more swallows in which rigorous statistical models (Nichols et al. 1994) are used to estimate survival would be highly instructive for testing the negative relationship that may exist between fecundity and survival in these and possibly other passerines (Martin 1995).

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APPENDIX. Comparative nestling growth statistics for North American and European populations of hirundinids. K and t_{10-90} were calculated using Ricklefs (1967) graphical method. R is the ratio of asymptotic nestling mass to adult mass.

Species	Mass (g)		K	t_{10-90}[a] (days)	R	Location	Source[b]
	Adult	Asymptote					
Progne subis	50.2	60.0	0.385	11.40	1.20	Kansas	1
Hirundo rustica	17.8	20.5	0.453	9.70	1.15	New York	1
	19.6	21.6	0.432	10.20	1.10	New York	2[c]
	19.6	20.7	0.412	10.80	1.06	New York	2[d]
	19.6	21.5	0.496	8.85	1.10	New York	3
Hirundo pyrrhonota	20.1	27.0	0.426	10.30	1.34	New York	1
	23.4	28.5	0.490	9.00	1.22	New York	3
Delichon urbica	19.4	24.8	0.418	10.50	1.28	England	4
Tachycineta bicolor	21.1	22.0	0.488	9.00	1.04	New Brunswick	1
	20.1	22.6	0.502	8.74	1.12	Manitoba	5
	21.6	23.8	0.526	8.35	1.10	Ontario	6[e]
	21.6	21.5	0.514	8.54	1.00	Ontario	6[f]
	21.6	23.0	0.510	8.61	1.09	New York	3
Tachycineta thalassina	14.8	21.5	0.410	10.70	1.45	Washington	1
Stelgidopteryx serripennis	15.6	18.5	0.458	9.60	1.18	Michigan	1
Riparia riparia	13.7	16.4	0.523	8.40	1.20	England	7

[a] Indicates the time required to complete between 10% and 90% of asymptotic mass.

[b] Code to references: 1 = Ricklefs 1968; 2 = Shields and Crook 1987 ([c] and [d] refer to parasite-free and parasitized young); 3 = this study; 4 = O'Connor 1978; 5 = Zach and Mayoh 1982; 6 = Quinney et al. 1986 ([e] and [f] refer to high food and low food environments); 7 = Turner and Bryant 1979.

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WINTER HABITAT OF KIRTLAND'S WARBLER: AN ENDANGERED NEARCTIC/NEOTROPICAL MIGRANT

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ABSTRACT.—Habitats of Kirtland's Warbler (*Dendroica kirtlandii*) on the wintering grounds in the Bahama Archipelago are presented based upon data from 29 specimens, two bandings, and 67 sightings of at least 61 individuals on 13 islands scattered through the region. We placed a major emphasis on a study site in central Eleuthera, with additional information from sites on Grand Turk, North Caicos, and Crooked Island. The warblers used upland habitats that have a low shrub/scrub component with a mosaic of small openings and openings within the vegetation at the ground level. Six broad habitats were used: natural shrub/scrub, secondary shrub/scrub, low coppice, pineland understory, saline/upland ecotone, and suburban; high coppice was not used. The structure and floristic composition of the habitats are described. Observations (n = 451) of a Kirtland's Warbler male (uniquely color banded) and female over three months indicated the birds generally stayed within 3 m of the ground (98% of observations), and used a territory of 8.3 ha. A crude estimate of potential winter habitat suggests that not only is there more than an adequate amount in the Bahama Archipelago for the current small population of warblers (733 singing males in 1997), but also enough for a considerably larger population. No serious future threat to the amount of that habitat is foreseen. *Received 5 May 1997, accepted 13 Jan. 1998.*

Kirtland's Warbler (*Dendroica kirtlandii*) breeds in the Upper Peninsula (rarely) and northern Lower Peninsula of Michigan and winters in the Bahama Archipelago (Fig. 1) (Mayfield 1960, 1972, 1992, 1996; Radabaugh 1974; Clench 1978; Walkinshaw 1983; Sykes 1989; C. I. Bocetti and J. Weinrich, pers. comm.). The small population (200 singing males during the breeding season in 1976, 219 in 1977, 215 in 1984, and 217 in 1985 during periods of this study; more recently 766 in 1995, 692 in 1996, and 733 in 1997; Weinrich 1995, pers. comm.) is widely dispersed in the islands during winter. On the wintering grounds the species is a skulker in low, dense vegetation and does not sing, but will give loud chip notes similar to those of the Ovenbird (*Seiurus aurocapillus*). Surveys for passerines in the Bahamas have located only four Kirtland's Warblers before this study in 1985 and 1986 (Van Tyne 1951; Van Tyne and Mayfield 1952; Paulson 1966; Mayfield 1960, 1972, 1992; Radabaugh 1974; Emlen 1977; Clench 1978; Buden 1987a, 1987b, 1990, 1992a, 1992b). Since the end of extensive collecting in the late 1800s and early 1900s, most warblers have been located by chance. Except for observations by Radabaugh (1974) on Crooked Island (<2 h on 3 days over a 12-day period), and Sykes' work on Eleuthera, all sightings of this species in winter have been brief one-time events. For this reason, little has been published on the winter habitat of Kirtland's Warbler. Mayfield (1972, 1996) summarized what little was known of the warbler's winter habitat, Radabaugh (1974) described the site where he found a bird in March 1973 on Crooked Island, and Clench (1978) briefly described where she observed a warbler in February 1978 on North Caicos. Because this endangered species spends at least 40%–60% of the year on its wintering grounds (Mayfield 1972, 1992; Walkinshaw 1983; Sykes et al. 1989), it is important for its long-term management and conservation to know more about its habitat requirements. In this paper we summarize what is known of the winter habitat of Kirtland's Warbler and report our more recent findings on the subject.

STUDY AREA

The Bahama Archipelago consists of the islands of the Commonwealth of the Bahamas and the British Crown Colony of the Turks and Caicos Islands in the British West Indies. They rise from a multisectioned platform of shallow-water marine limestones on a northwest-southeast axis spanning some 1,012 km. The islands extend from 20° 55′ to 27° 30′ N latitude and from 71° 10′ to 79° 20′ W longitude and lie within the East Trade Wind belt of the western North Atlantic

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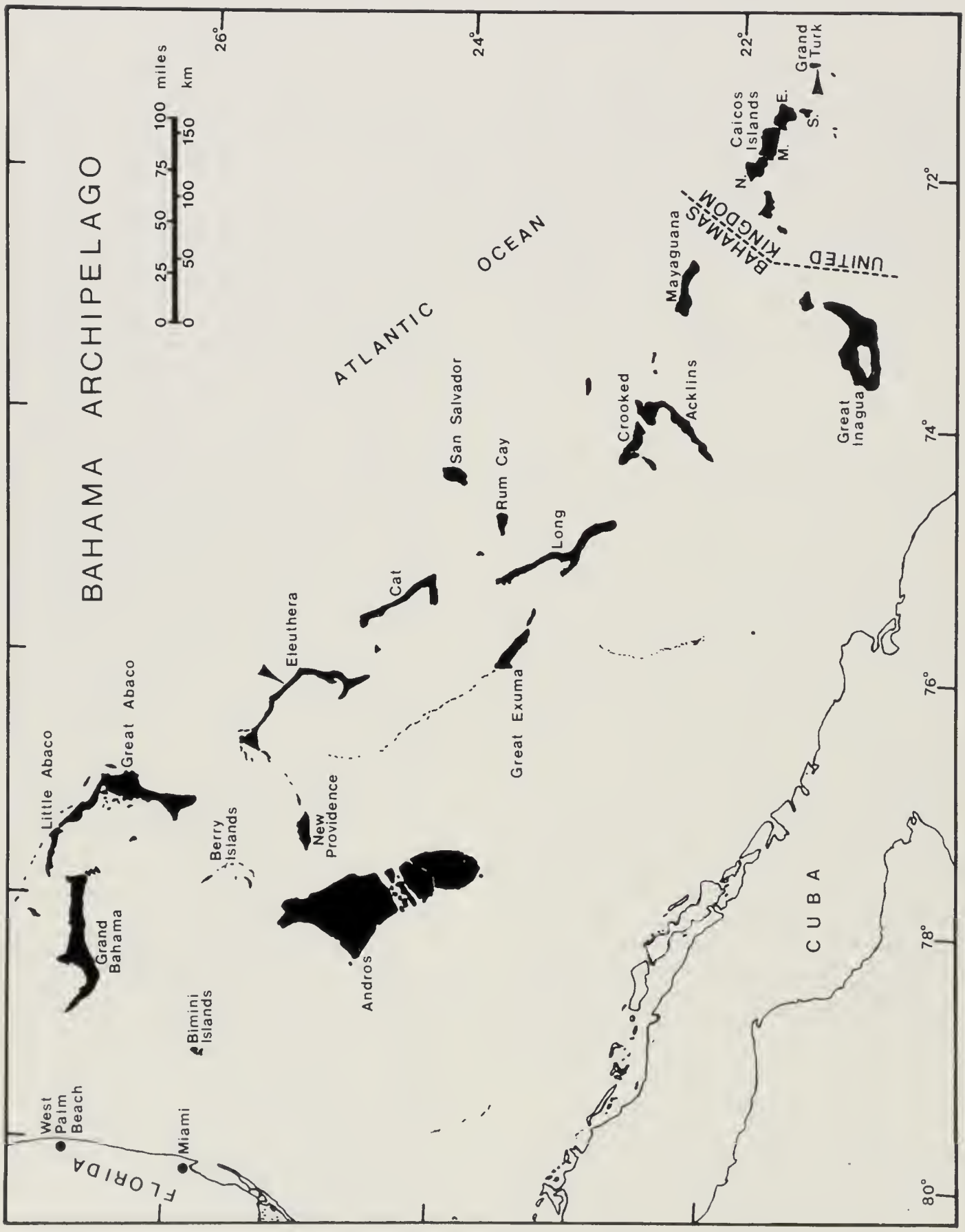
(Gillis 1977, Correll and Correll 1982, Sealey 1994). The islands have relatively low topography (maximum elevation above sea level is 64 m on Cat Island), and are geologically similar and distinctly oceanic. Floristically, they are also similar, although the northern islands with pine forest (*Pinus caribaea*) are more mesic, and the drier islands to the south are covered by dense scrub. The archipelago encompasses 260,000 km^2 and has 35 major islands, about 700 cays, and an estimated 2400 exposed rocks that have some type of vegetation. The land mass is approximately 14,500 km^2. The climate is tropical (no record of freeze): Grand Bahama (Freeport, 1973–1982), mean annual temperature 24° C, mean annual range 17–29° C; Great Inagua (Matthew Town, 1973-1982), mean 26° C, range 22–29° C (N. E. Sealey, pers. comm.); and Grand Turk, mean 27° C, range 16–36° C (Pearce and Smith 1990). Rainfall is highest in the north, decreasing southeastward: Grand Bahama (Freeport, 1973–1990), mean annual rainfall 141 cm, mean annual range 92–186 cm; Great Inagua (Matthew Town, 1973–1990), mean 67 cm, range 31–99 cm (N. E. Sealey, pers. comm.); and Grand Turk, mean 73 cm (no range available; Pearce and Smith 1990). The islands have an annual rainfall cycle, are subject to hurricanes, and are generally wettest from May through November. Rainfall varies between years on any given island and between islands at the same latitude. The Bahamas have no surface-flowing freshwater streams or rivers nor large freshwater lakes (Gillis 1977, Correll and Correll 1982). The highly variable landforms are well described in Sealey (1994). The primary island landscapes are ridges formed from old dunes and relatively flat rocklands formed from limestone deposits. Secondary landscapes include coastal cliffs and headlands, wave–cut platforms, dunes, beaches, and coastal and inland wetlands. Kirtland's Warbler habitats occur mainly on the two primary landscapes.

Bahamian vegetation has been seriously altered since the Eighteenth Century (Mooney 1905). After 1718, when pirates had been subdued, European settlers made widespread attempts at agriculture on many of the islands. The land was planted to cotton and later with other crops like sisal, citrus, tobacco, and tomatoes. After the abolition of slavery in 1834, little commercial agriculture continued and the land reverted to scrub, but the damage to native habitats had been done. Today Bahamian agriculture is largely limited to individual farm plots cleared in the scrub, where the thin remaining soil lies in depressions in the surface limestone. The history of land use in the Bahamas is yet to be thoroughly documented, but the ravages of the early attempts at agriculture are clearly evident. Today, as one walks over the stony ground and pavement limestone of uninhabited scrub, the soil is gone (if it was ever there), yet wild cotton plants still grow on some islands (Clench, pers. obs.).

The biotic communities in the archipelago have been classified into a number of broad categories. Gillis (1977) referred to five major vegetation types: pineland, coppice, scrubland, strand, and mangrove, but did not mention freshwater communities or salt marshes. Correll (1979) and Correll and Correll (1982) recognized the following generalized plant communities: coastal rock, sand strand and *Uniola*, coastal coppice, whiteland (low dunes and flats), fresh water, tidal flats and salt marshes, mangrove, blackland (includes high and low coppice), and pineland (wet and dry barrens). With some modifications, we have used the works of Gillis (1977) and Correll and Correll (1982), plus our own field experience in the islands to describe the six habitat types in which Kirtland's Warblers have been found.

The habitats described herein are based upon sites where Kirtland's Warblers have been found throughout the archipelago, 1879 through 1994, but with emphasis on our work on Eleuthera, Grand Turk, and North Caicos. Several additional reports (specimens and sightings) could not be assigned to a habitat type because of insufficient data. Descriptions of the habitats include some general physiognomic characteristics and dominant floristic composition. These upland, mostly well-drained, habitats include: (1) natural shrub/scrub, (2) secondary shrub/scrub, (3) low coppice, (4) pineland understory, (5) saline/upland ecotone, and (6) suburban. The term coppice is widely used throughout the Bahamas and refers to the mostly tropical broad-leaved mixed evergreen-deciduous woodlands in which most of the plant species can propagate from stumps and roots as well as from seeds. Common names of plants are used throughout. (An alphabetical listing of all plants by common name, scientific name and family, growth form, status, and maximum height is given in the Appendix). Vernacular and scientific names mostly follow Correll and Correll (1982). The six principal Kirtland's Warbler wintering habitats are described as follows.

Natural shrub/scrub (coastal coppice).—Also known as sand *Coccothrinax*-shrub community, silver palm association, or *Erithalis-Reynosia* association (Correll and Correll 1982), natural shrub/scrub is low-growing because of natural environmental conditions. Vegetation generally ranges from 1–4 m in height, often with scattered taller emergent plants, on flat or gently rolling topography, and on substrate of sand, mixed sand and fractured limestone, or limestone rock. Depending on its location, this habitat may be exposed to periodic high winds, fire, flooding, and salt spray, all of which tend to retard growth of the woody species. Thus, most plants are bush-like or shrubby in growth form. A mosaic of openings of varying sizes and shapes, with ground cover or exposed substrate, may or may not be present. Silver thatch palm may occur. Other primary plants include black bead, black torch, cocobey, coco plum, darling plum, joe-wood, myrsine, narrow-leaved blolly, poison wood, sea grape, small-flowered prickly apple, Spanish stopper, spreading torch, torchwood, touch-me-not, wild guava, wild saffron, wild sage (widely known as lantana), and woolly corchorus. Morning glory and smooth passion-flower vines as well as ground covers of black-headed


BAHAMA ARCHIPELAGO
0 25 50 75 100 miles
0 50 100 150 km
26°
24°
22°
72°
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76°
78°
80°
ATLANTIC OCEAN
CUBA
FLORIDA
West Palm Beach
Miami
Bimini Islands
Grand Bahama
Little Abaco
Great Abaco
Berry Islands
New Providence
Andros
Eleuthera
Cat
Great Exuma
Long
Rum Cay
San Salvador
Crooked
Acklins
Mayaguana
BAHAMAS
UNITED KINGDOM
Great Inagua
Caicos Islands
N.
M.
E.
S.
Grand Turk

sedge and *Fimbristylis* also are common (Correll and Correll 1982).

Secondary shrub/scrub.—This habitat occurs as the direct result of human activities; it usually develops on subsistence farms (on which slash-and-burn techniques were used) after they have been abandoned, most often in areas that were coppice (mainly blacklands; see Correll and Correll 1982). Thus, this habitat is an early stage of seral vegetative succession, and in the northern islands may be dominated for a period by wild sage. Vegetation generally ranges from 1.0–1.5 m in height, with bushy growth form, often with taller emergent individual plants; it grows on flat, gently rolling topography or on ridge slopes, and on substrates of thin pockets of lateritic and black soils, exposed limestone rock, fractured limestone, etc. This habitat is generally more sheltered from wind and salt spray than is natural shrub/scrub. In addition to wild sage, some of the more common plants are black bead, black torch, broom-bush, cinnecord, coco plum, darling plum, gumbo-limbo, mahogany, myrsine, pigeon plum, poison wood, Spanish stopper, torchwood, white stopper, and woolly corchorus. As with natural shrub/scrub, there is often a mosaic of openings of various sizes and shapes with ground cover and exposed substrate.

Low coppice.—Low coppice is the younger or shorter growth of the whiteland and blackland communities of Correll and Correll (1982) in which the height of the vegetation is shorter than 4.6 m (15 feet), as originally described by Coker (1905). High coppice is over 4.6 m in height. Whiteland is generally near the coasts, while blackland is usually in island interiors. The southern islands of the archipelago have relatively more whiteland coppice than do the northern islands.

Whiteland substratum is typically sterile coral sand that forms low dunes and flats of hard-packed light gray soils. Where it is inland, it becomes somewhat loamy, but overall it is poor in nutrients and moisture retention. Whiteland soils contain lime and rock and support a hardier assemblage of plants, but the forest itself is impoverished compared to that on blacklands (Correll and Correll 1982, Campbell 1991). The dominant plants of whitelands are black bead, cinnecord, darling plum, joe-wood, lignum vitae, narrow-leaved blolly, poison wood, whitewood, wild dilly, and wild saffron as well as a number of epiphytes (Correll and Correll 1982).

Blackland includes most of the rolling hills, highest ridges, and flatlands inland of the coast. It frequently has solution or sink holes (called "banana holes" because they are large enough to hold one or more banana plants) and has the greatest plant diversity and density of all the broad habitat types in the archipelago. Most soil is black, with limited areas of red loam. These fertile soils are the most heavily used for agriculture and are formed from a mixture of weathered substratum and organic matter. A few of the several hundred dominant trees and shrubs include bitter bush, black ebony, cow-bush, crabwood, gumbo-limbo, jumbie bean, logwood, mahogany, maiden bush, quicksilver-bush, rat-wood, short-leaved wild fig, soap-berry, strangler fig, strong back, sweet torchwood, white ironwood, and wild tamarind, plus many species of ferns and terrestrial orchids (Coker 1905, Correll and Correll 1982).

Pineland understory.—The pinelands are confined to the northern islands (Grand Bahama, Great Abaco, Little Abaco, New Providence, and Andros; formerly included the Berry Island group), with a widely disjunct occurrence in the southern islands of Pine Cay, North Caicos, and Middle Caicos. This habitat is dominated by a single species, the Caribbean pine. The pine stands are characterized by broken/open canopy and widely spaced trees, and are divided into two types, wet and dry pine barrens. In wet pine barrens, the substratum is typically honeycombed limestone with the water table (usually a lens of fresh water overlying brackish) within a few centimeters of the surface. The presence of cabbage palm is an indicator of the wet pine barrens. The pines generally form the main canopy, while all other trees and shrubs make up the understory stratum, among which are black bead, candle-berry, narrow-leaved blolly, pigeon plum, poison wood, princewood, strong-back, wild sage, and woolly corchorus. Among the vines and herbs are auricled green-brier, finger-grass, mangrove swamp vine, prickly green-brier, and wild yam (Correll and Correll 1982).

Wet and dry pine barrens are often intermixed, but silver thatch palm replaces cabbage palm in the dry barrens. The same species of plants may be present in both wet and dry barrens, but the following are more prevalent in the dry type: bastard stopper, cinnecord, cocobey, common ernodea, pigeonberry, poison wood, St. Andrew's cross, southern bracken fern, tetrazygia, vernonia, wild lime, and yellow alder (Correll and Correll 1982). For a more detailed description of pinelands, see Emlen (1977).

Saline/upland ecotone.—This is the transition zone between the salt marsh and mangrove communities and the upland coppice; it occurs on relatively flat terrain and is often subject to flooding with salt water during extreme high tides and intense storms, and washed with fresh water during heavy rains. This is a saline-to-brackish habitat with a substrate of pavement limestone, broken limestone fragments, marl and sand mixture, etc., generally on the leeward (west) sides of

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FIG. 1. The winter range of the Kirtland's Warbler in the Bahama Archipelago with study sites on Eleuthera, Bahamas (2.1 km NW of Governor's Harbour) and Grand Turk (south end of island near airport) shown by black arrowheads.

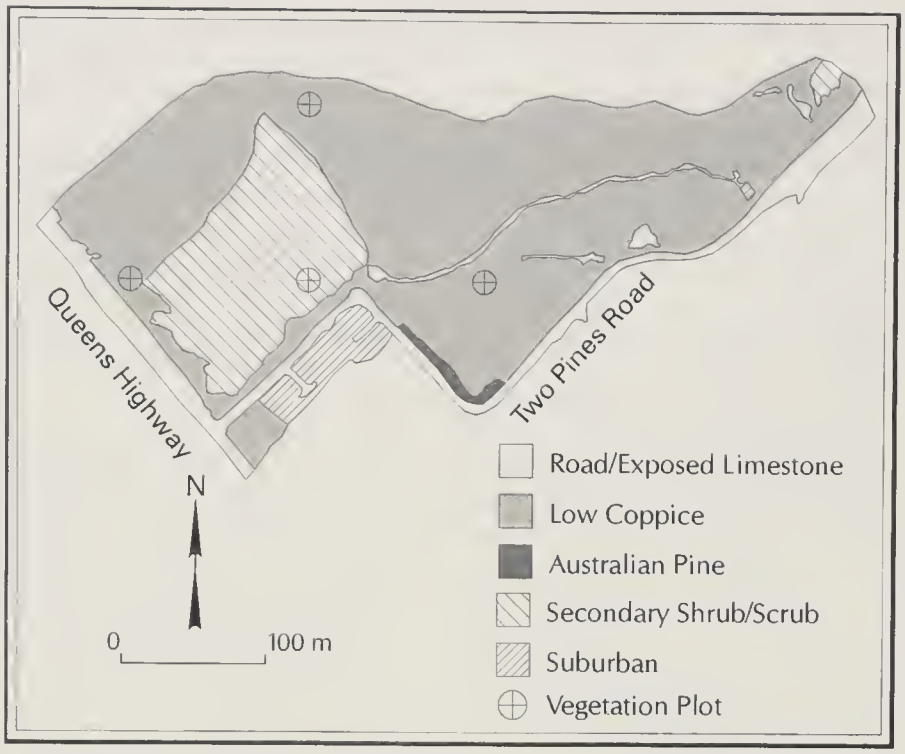

FIG. 2. Winter territory of a uniquely color-banded (in 1985) male and an unbanded female Kirtland's Warbler on Eleuthera 1985 and 1986, based on 451 sightings of the two birds, plus five mist-net captures of the male. The four vegetation plots within the territory are shown.

the islands. Vegetative zonation within this habitat forms a mosaic of shrub/scrub patches or stands of trees interspersed with bare substrate or ground cover. Because the archipelago contains so many islands, and most have this ecotone in abundance (W. T. Gillis, pers. comm.), it is an important component of Bahamian habitats. Some of the more abundant plants include black mangrove, bonita, broom-bush, buttonwood, cat's claw, horse bush, joe-wood, saltwort, sea grape, sea ox-eye, seashore rush-grass, seaside purslane, spurge, varnish leaf, wild sage, and woody glasswort.

Suburban.—This habitat occurs on the well-drained sites of human habitation within any of the principal upland natural habitats; it consists of buildings (homes, cottages, etc.) surrounded by mowed/grazed lawns with mixed plantings of native and/or introduced shrubs and trees. Among some of the common introduced plants are Australian pine, avocado, bougainvillea, Chinese hibiscus, common oleander, copper leaf, croton, frangipani, various lawn grasses, ixora, Japanese pittosporum, mango, natal-plum, Norfolk Island pine, orange-jessamine, orchid-tree, many species of palms, powder-puff, red periwinkle, royal poinciana, scarlet sage, trailing wedelia, and weeping bottlebrush.

METHODS

Eleuthera study site.—A study area was established in late February 1985 by Sykes and Paul R. Sievert 2.1 km NW of Governor's Harbour (Figs. 1 and 2) on Eleuthera where they had found a male Kirtland's Warbler 22–28 February 1985. This bird was captured and uniquely color-banded (U. S. Fish and Wildlife Service aluminum band no. 2020-67020 above an unnumbered red band on the left leg and unnumbered green over red on the right leg). Data from this warbler are central in this paper and other reports in preparation. The study site (25° 12′ 41″ N, 76° 15′ 20″ W) is located at the intersection of Queens Highway and Two Pines Road (Figs. 2, 4). From mid-December 1985 through late March 1986, Sykes, David A. Jett, William H. Howe, and Daniel M. Taylor studied the banded male (present 19 December 1985 through at least 28 March 1986) and a female (present 18 December 1985 through 23 January 1986) on winter territory at this locale. The territory consisted primarily of shrub/scrub, low coppice, and suburban habitats; it extended from the crest of the central limestone ridge on the lee (southwest) side of the island downslope, averaging about 5%, to Queens Highway (a two-lane paved road running the length of the island). This is the only intensively studied Kirtland's Warbler site in the archipelago. The territory was mapped and analyzed using a combination of remote sensing and geographic information system (GIS) techniques. Habitat types were interpreted from false color infrared aerial photographs acquired at a scale of 1:10,000 on 3 June 1987. A portion of a single positive transparency covering the warbler's territory was scanned at 600 dots per inch (dpi) and transferred to the Desktop Mapping System (DMS)™ software package operating on a Pentium personal computer. Geocoding procedures of the DMS were used to rectify the scanned photograph to the Universal Transverse Mercator (UTM) ground coordinate system within ±5 m root-mean-square-error (RMSE) using ground control obtained from the 1:25,000 scale Bahamas Dept. of Lands and Surveys

map (1975). Planimetric mapping of habitat types was then performed by digitizing vegetation and land use boundaries on-screen using the scanned air photo as a backdrop. Habitat types and land uses were classified as low coppice, secondary shrub/scrub, Australian pine, suburban, and road/exposed limestone. The digital vector data for habitat and land use boundaries within the Kirtland's Warbler territory were captured in ARC/INFO format for direct input to the GIS system. ARC/INFO, resident on a SUN Sparc 10-512 workstation, was used to edit the digital file, enter habitat information, and create a GIS coverage. Areal statistics summarizing the total coverage of each habitat type were then derived using ARC/INFO procedures and a hardcopy plot of the territory created.

Grand Turk study sites.—Two study areas, about 1 km apart, were established by Sykes and Sievert for short periods near the southern end of Grand Turk Island (Fig. 1) at sites where two individual Kirtland's Warblers were each seen once for several minutes. One site (21° 26′ 44″ N, 71° 08′ 08″ W) in natural shrub/scrub (male seen 7 March 1985 by Sykes) was north of the Grand Turk Airport runway. Three mist nets were used 7–10 and 14–15 March 1985, but no Kirtland's Warblers were captured. The second site (21° 26′ 25″ N, 71° 08′ 33″ W) in saline/upland ecotone (male seen 11 February 1985 by Sievert) was south of Grand Turk Airport runway, but no mist netting was done.

Vegetation sampling.—Vegetation was sampled on Grand Turk in March 1985 and on Eleuthera in January through March 1986. Circular 0.04-ha plots were sampled using techniques described by James and Shugart (1970) with some modifications. Foliage density was measured with a density board held vertically at 11.3 m from the center of the plot at the four cardinal directions (Noon 1981). On Grand Turk, the first of each cluster of five plots was placed where a Kirtland's Warbler had been seen, and the remaining four plots were randomly located around the site at various distances from the reference plot. The first plot on Eleuthera was placed centrally in the habitat where two Kirtland's Warblers were seen frequently, and the remaining four plots (Kirtland's seen on three of the four) were 125 m (center to center) in each of the four cardinal directions from the reference plot.

Elevations at the plot centers were determined from topographic maps [Grand Turk: Turks and Caicos Islands, Series E8113, Dept. of Surveys 209, Turks Islands Sheet 14B, Edition 2, 1973; Eleuthera: Commonwealth of the Bahamas, Series 314, Dept. of Lands and Surveys, Eleuthera Sheet 14B, Edition 1, 1975; contour interval for both maps was 25 feet (7.6 m)] with a scale of 1:10,000 (Grand Turk) and 1:25,000 (Eleuthera). Slope was estimated at each site (amount of drop per 30 m) and distance to the nearest different habitat was measured to the nearest whole meter from plot centers. A tree was defined as having a diameter at breast height (dbh; 1.37 m above ground) of at least 3 cm and usually with one main stem, and a shrub was 0.5 m or less in height with one or multiple stems less than 3 cm dbh. Ground cover was less than 0.5 m in height. A density board 0.5 m wide and 3 m tall was divided into four height intervals (0–0.3 m, 0.31–1.0 m, 1.1–2.0 m, and 2.1–3 m). Foliage density measurements for the lower two intervals were taken from a kneeling position and those from the upper two intervals from a standing position, all from the center to the edge of the plot along the four cardinal directions. Foliage density was then recorded as the number of squares (10 × 10 cm each) in each height interval at least 50% obscured by green foliage (details in Noon 1981). Another estimate of foliage density, which we refer to as vertical foliage cover, was made at the precise site within the vegetation used by foraging warblers. Vertical foliage cover was determined by imagining the foraging bird at the center of a 1-m diameter sphere and estimating the percentage of cover (0, 20, 40, 60, and 80) around the bird within the sphere if superimposed upon a vertical plane bisecting the sphere. Canopy, shrub and ground cover, leaf litter, bare soil, and exposed rock were determined by counting the number of hits out of a total of 40 along the four cardinal directions (10 each at 1 m intervals along line transects). Dominant shrub and ground cover were based upon greatest number of stems per plot, the second most abundant shrub being the subdominant.

With W. T. Gillis, Clench visited Radabaugh's 1973 site on Crooked Island on 18 March 1976. They collected botanical specimens, took habitat photographs, and made notes on the habitat type. On 10 February 1978, Clench took plant samples, notes, and photographs at the North Caicos Island site the day after she saw a female Kirtland's Warbler there. The plant samples were later sent to Gillis for identification.

The study of Kirtland's Warbler in the Bahama Archipelago by the U.S. Fish and Wildlife Service was planned for three years, but because of problems that arose beyond the team's control, the project was terminated before the first field season was completed; there was no funding thereafter. Hence, the sample sizes are small, precluding statistical analysis.

RESULTS

Winter habitats used by Kirtland's Warbler in the Bahama Archipelago are based on 98 observations (Table 1), including data from 29 specimens, two bandings, and 67 sightings. These 98 observations represent at least 61 individual warblers. The majority of the specimens were collected by C. J. Maynard (Mayfield 1960) on New Providence before 1900, and most sightings were made on Eleuthera (mainly this study), with the remainder of the sightings distributed among 11 other islands with one to six occurrences each.

Six broad habitats were identified as used by wintering Kirtland's Warblers: natural shrub/scrub, secondary shrub/scrub, low cop-

TABLE 1. Specimens, bandings, and sightings of Kirtland's Warblers in the Bahama Archipelago for which the general habitat type is known.[a]

Island	Number			
	Specimens	Bandings	Sightings	Total
Andros	1		1	2
Cat	1			1
Cat Cay[b]			1	1
Crooked			1	1
Eleuthera		1	43[c]	44
Grand Bahama		1	3	4
Grand Turk			3	3
Great Abaco			3	3
Great Inagua			3	3
New Providence	26		8	34[d]
North Caicos			1	1
San Salvador	1			1
Total 12	29	2	67	98[e]

[a] Data from the literature and unpublished reports through 1994 and this study.
[b] Cat Cay lies approximately 16 km south of South Bimini on the western edge of the Great Bahama Bank.
[c] Includes multiple recaptures and sightings of an uniquely color-banded male and accompanying unbanded female as a part of this study, plus sightings by other observers of four unsexed individuals at other localities on Eleuthera over the years.
[d] Includes Paradise (Hog) Island (two sightings).
[e] This number represents 61 individual Kirtland's Warblers.

pice, pineland understory, saline/upland ecotone, and suburban. The shrub/scrub category (Table 2), a combination of natural and secondary shrub/scrub, and low coppice are the most frequently recorded, but it should be kept in mind that the habitats and islands have not been systematically surveyed. Most reports, aside from our study site on Eleuthera, have come from incidental observations on those islands most readily accessible and favored by birders and ornithologists (Mayfield 1972). Over the past 100 years or so, reports have been sporadic with few or no details as to specific location, habitat, behavior, or plumage. No Kirtland's Warblers have been reported in high coppice, although it is frequented by other wintering warblers. The suburban habitat is probably of little importance to Kirtland's Warbler (Clench and Sykes, unpubl. data) in winter but may be used on occasion when adjacent to one of the favored habitats; it is, however, frequented by visiting birders. Saline/upland ecotone and, perhaps, pineland understory are probably of greater importance than the small sample indicates.

The diversity and structure of warbler winter habitats are shown in Figures 3 and 4. All of these communities have a well-developed shrub layer interspersed with many small irregularly shaped openings (also descriptive of

TABLE 2. Habitats in which Kirtland's Warblers have been reported in the Bahama Archipelago.[a]

Island	Occurrences[b]					
	Habitat					
	Shrub/scrub[c]	Low coppice	Pineland understory	Saline/upland ecotone	Suburban	Total
Andros		2				2
Cat	1					1
Cat Cay	1					1
Crooked				1		1
Eleuthera	3	5			2	10
Grand Bahama[d]		2	1		1	4
Grand Turk	2			1		3
Great Abaco[d]	1	2				3
Great Inagua	1	2				3
New Providence	27	6	2			35
North Caicos				1		1
San Salvador		1				1
Total	36	20	3	3	3	65

[a] Many specimen records and reported sightings are not included; their information was insufficient to determine habitat category.
[b] Most numbers represent different individual Kirtland's Warblers; two individuals studied on Eleuthera were seen using three different habitats.
[c] Both natural and secondary shrub/scrub combined; most accounts were not detailed enough to distinguish between the two.
[d] There is a problem of correct identification of many sightings on these islands (Sykes and Kepler, unpubl. data); all such reports have been excluded from the paper.

FIG. 3. Habitats at selected sites where Kirtland's Warblers have been observed in the Bahama Archipelago in winter. A. Natural shrub/scrub at lighthouse at Hole in the Wall, Great Abaco (25° 51′ 32″ N, 77° 11′ 02″ W), sighting January 1989 (R. S. Gnam, pers. comm.). B. Low coppice invaded by non-native plants with overstory of Australian pine on northwest edge of golf course along nature trail, Paradise (Hog) Island (22° 05′ 08″ N, 77° 18′ 06″ W), sighting 2 February 1985 (J. A. Gerwin and L. G. Sorenson, pers. comm.). C. Pineland understory southeast of Nassau International Airport, New Providence (25° 00′ 36″ N, 77° 27′ 05″ W), sightings 13 December 1989 and 1992 (P. W. and S. A. Smith, pers. comm.) and sighting in same general area 20 August 1970 by R. W. Schreiber and G. E. Woolfenden (Robertson 1971; G. E. Woolfenden, pers. comm.). D. Saline/upland ecotone about 900 m north of south shoreline and halfway between Brown's Settlement and Cove Point, Crooked Island (22° 43′ 07″ N, 74° 01′ 45″ W), sightings of same bird 11, 12, and 22 March 1973 (Radabaugh 1974, pers. comm.). E. Saline/upland ecotone about 335 m northwest of Bellefield Landing, North Caicos (21° 54′ 30″ N, 72° 02′ 00″ W), sighting 10 February 1978 (Clench 1978). F. Natural shrub/scrub 75 m north of airport perimeter fence near east end of runway and just south of old canal between south end of Great Salina complex and South Creek, Grand Turk (21° 26′ 42″ N, 71° 08′ 09″ W), sighting 7 March 1985 (Sykes). All photographs reproduced from color transparencies; A and F by Sykes, B by A. W. White, C by S. A. Smith, and D and E by Clench.

FIG. 4. Winter territory of an uniquely color banded male Kirtland's Warbler 1984–1985 and 1985–1986 and an unbanded female 1985–1986. This is the study site 2.1 km northwest of Governor's Harbour, Eleuthera (25° 12′ 41″ N, 76° 15′ 20″ W) at the intersection of Queens Highway and Two Pines Road. A. Low coppice, typical of much of the habitat within this warbler territory. Vegetation in center of this photo is where the male was first discovered along the edge on Two Pines Road in 1985. B. Overview of the territory at the lower elevation with secondary shrub/scrub surrounded by low coppice with Australian pine saplings projecting above the shrub and coppice layers. C. Low coppice in background interfacing secondary shrub/scrub of mostly wild sage. D. Mist net lane in stand of wild sage. E. Secondary shrub/scrub showing height (note meter stick held in right hand) and relative density of vegetation. This was the center of the first vegetation plot in study area. F. The ground level with leaf litter showing the general openness beneath secondary shrub/scrub, most of which is wild sage. Photos by Sykes 1985 and 1986.

breeding sites in Michigan). The shrub layer is often open at ground level (Fig. 4F). In both the natural and secondary shrub/scrub where warblers have been recorded, the vegetation is relatively easy to walk through. Suburban habitat, while highly modified and fragmented, also contains these key elements in the form of plantings and expanses of trimmed

grass or bare substrate. In strong contrast, most Bahamian habitats are densely vegetated and difficult to traverse.

Kirtland's Warbler winter territories on Eleuthera (8.3 ha) and on Crooked (about 6.9 ha) are larger than breeding territories in Michigan. Mayfield (1960) reported a mean Michigan territory of 3.4 ha (range, 0.6–6.7 ha) from 20 sites, and Sykes, C. B. Kepler, and C. I. Bocetti (unpubl. data) found 38 breeding territories to have a mean of 2.7 ha. This may result from more (perhaps poorer quality) habitat being available and/or lower density of warblers in winter than on the breeding grounds, where the territories are clumped in loose colonies. It could also simply be the result of the small sample of wintering territories.

At the winter territory study site on Eleuthera in 1985 and 1986 (Figs. 2 and 4), the 8.3-ha territory consists of 74.8% low coppice, 19.3% secondary shrub/scrub, 3.4% suburban habitats, 1.7% openings (old clearings $\geq 10^2$ m with exposed limestone substrate), and 0.8% Australian pine (planted in a strip along Two Pines Road). While the warblers were seen in all three habitats and the two miscellaneous categories, 98% of the observations were of birds in secondary shrub/scrub and low coppice.

Ninety-eight percent of all foraging (n = 448 observations) of the two warblers on Eleuthera was from the ground up to 3 m. Only 2% of foraging was between 3 to 6 m, and none was higher than 6 m. Vertical foliage cover at the point where a warbler was foraging was estimated to the nearest 20%. The cover usage ranged from 25 observations in zero (completely open) cover, 50 in 20%, 114 in 40%, and 18 in 60% (n = 207 observations); none was greater than 60%. Seventy-five percent of all foraging observations in vegetation were in wild sage (Table 3), with the remainder distributed among 10 other plant species (331 observations). Additional foraging occurred on the ground (Sykes, unpubl. data).

The structure of the secondary shrub/scrub and low coppice based upon vegetation plot measurements at the study sites in the Eleuthera and Grand Turk territories is summarized in Table 4. On Eleuthera, the slope ranged from 0–5% in the four plots. Few trees (25/ha) were present in the secondary shrub/scrub, whereas the low coppice had a mean of 2248/ha. Shrub density in secondary shrub/scrub was 54,711 stems/ha (1 plot), with a shrub cover of 50%; in low coppice the mean was 31,246 stems/ha (3 plots) with 62% cover. Mean ground cover was relatively low, with 14% in secondary shrub/scrub and 25% in low coppice, as was mean bare soil at 18% and 7%, and mean exposed rock at 15% and 17%. Mean leaf litter was higher at 68% and 77%. Mean foliage density (as measured by the density board) from ground level to 1 m in height was about 100% and decreased thereafter as the height increased. Of the two Eleuthera habitats, canopy was present only in low coppice. Mean shrub height in the secondary shrub/scrub was 1.1 m; this measurement was not taken in low coppice which had a mean canopy height of 3.3 m.

TABLE 3. Species of plants in which two Kirtland's Warblers were observed foraging (n = 331 observations) at one territory on Eleuthera winter 1986.

Common name	Scientific name	Percent observations
Wild sage	*Lantana involucrata*	76
Soldier-bush	*Tournefortia volubilis*	8
West Indian snowberry	*Chiococca alba*	4
Cinnecord	*Acacia choriophylla*	3.5
Black torch	*Erithalis fruticosa*	3.3
Wild lime	*Zanthoxylum fagara*	1.8
Australian Pine	*Casuarina equisetifolia*	1
Wild cassada	*Bumelia salicifolia*	0.9
Black bead	*Pithecellobium keyense*	0.9
Beef-bush	*Tabebuia bahamensis*	0.3
Slender nut-rush	*Scleria lithosperma*	0.3

At the natural shrub/scrub and saline/upland ecotone territories on Grand Turk (Table 4), the slope at the natural shrub/scrub vegetation plots ranged from 0–1% (5 plots) and at saline/upland ecotone it was zero (5 plots). No trees were present at these two sites. Mean shrub density in natural shrub/scrub was 8601 stems/ha with shrub cover of 68%, and in saline/ upland ecotone it was 10,611 stems/ha with shrub cover of 37%. Mean ground cover was low in natural shrub/scrub (11%), but high in saline/upland ecotone (45%) while mean leaf litter was 55% and 19%, respectively. Bare soil was high at both sites, with

TABLE 4. Structure of habitats within four Kirtland's Warbler winter territories at three sites on two islands. See Methods for definitions and measurement procedures.

	Habitats						
	Eleuthera (1 territory, male & female)			Grand Turk (2 territories, 2 males)			
	Secondary shrub/scrub (n = 1 plot)	Low coppice (n = 3 plots)		Natural shrub/scrub (n = 5 plots)		Saline/upland ecotone (n = 5 plots)	
Variable	Number	Range	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE
Elevation (m)	7.6	6.0–9.1	7.6 ± 1.4	2.4–2.5	2.4 ± 0.02	0	1.0 ± 0
Slope (%)	3	0–5	1.7 ± 1.7	0–1	0.4 ± 0.2	0	0 ± 0
Nearest habitat (m)	20	25–40	31.7 ± 4.4	48–100	66 ± 12	75–150	111 ± 16
Trees/ha	25	1112–3829	2248 ± 818	0	0	0	0
Shrub stems/ha	54,711	18,031–39,275	31,246 ± 1328	5607–15,438	8601 ± 1835	1457–18,896	10,611 ± 2887
Palms/ha	0	0–1482	580 ± 91.4	0	0	0	0
Shrub cover (%)	50	58–68	62 ± 3.1	53–78	68 ± 4.2	18–50	37 ± 5.3
Ground cover (%)	14	11–39	25 ± 8.0	0–25	11 ± 4.3	30–63	45 ± 7.0
Leaf litter (%)	68	70–80	77 ± 3.3	38–80	55 ± 7.4	10–33	19 ± 3.7
Bare soil (%)	18	0–18	7 ± 5.7	20–63	43 ± 6.9	68–83	77 ± 2.8
Exposed rock (%)	15	3–30	17 ± 4.6	0–15	1.5 ± 1.5	0–15	4 ± 2.9
Canopy cover (%)	0	28–73	50 ± 13	0	0	0	0
Foliage density 0–0.3 m ht. (%)	100	98–100	99 ± 0.7	100	100 ± 0	27–100	84 ± 14.4
Foliage density 0.31–1.0 m ht. (%)	100	98.5–99	99 ± 0.3	96–100	99 ± 0.7	31–71	60 ± 7.5
Foliage density 1.1–2.0 m ht. (%)	47	80–100	90 ± 33	54–87	69 ± 7.1	0–50	17 ± 9.1
Foliage density 2.1–3 m ht. (%)	0	77–100	85 ± 8	0–52	26 ± 11.4	0–47	9.4 ± 9.4
Mean canopy ht. (m)	—	2–5	3.3 ± 0.5	—	—	—	—
Mean shrub ht. (m)	1.1	—	—	1.0–1.2	1.1 ± 0.04	0.8–1.8	1 ± 0.19

TABLE 5. Principal shrub and ground cover in five Kirtland's Warbler winter territories.

Island	Warbler territory	Habitat	Veg.[b] plot	Species[a] Shrub Dominant	Species[a] Shrub Subdominant	Species[a] Ground cover Dominant
Eleuthera	1	Secondary shrub/scrub	1	wild sage	cinnecord	grass sp.
		Low coppice	1	cinnecord	wild sage	grass sp.
			2	wild sage	cinnecord	grass sp.
Grand Turk	2	Natural shrub/scrub	1	darling plum	cassia	seashore rush-grass
			2	darling plum	sea grape	seashore rush-grass
			3	sea grape	darling plum	borreria
			4	sea grape	spurge	borreria
			5	varnish leaf	spurge	seaside purslane
Grand Turk	3	Saline/upland ecotone	1	buttonwood	bonita	seashore rush-grass
			2	sea ox-eye	broom-brush	seashore rush-grass
			3	broom-brush	varnish leaf	seashore rush-grass
			4	spurge	varnish leaf	seashore rush-grass
			5	spurge	broom-brush	seashore rush-grass
Crooked[c]	4	Saline/upland ecotone	—[d]	buttonwood and black mangrove	—	woody grasswort and seashore rush-grass
North Caicos[e]	5	Saline/upland ecotone	—[d]	black olive	—	white-top sedge

[a] For scientific names and families see Appendix.
[b] No data on shrub and ground cover veg. plot 3 on Eleuthera.
[c] Territory of March 1973 (Radabaugh 1974) visited February 1976 by William T. Gillis and Clench.
[d] No vegetation sampling plots measured.
[e] Territory of February 1978 (Clench 1978).

means of 43% and 77%, respectively, but mean exposed rock was low (1.5% and 4%). Mean foliage density in natural shrub/scrub was circa 100% from ground level to 1 m in height, decreasing to 69% between 1–2 m, and to 26% between 2–3 m. Mean foliage density in saline/upland ecotone was 84% at the height of 0–0.3 m, decreasing to 60% at 0.3–1 m, 17% at 1–2 m, and 9.4% at 1–3 m. No canopy was present in either the natural shrub/scrub or saline/upland ecotone. Mean shrub height was 1.1 m and 1 m in the two Grand Turk territories.

Dominant shrub cover (Table 5) in the winter territory in secondary shrub/scrub (one plot) on Eleuthera was wild sage, with unidentified grasses as dominant ground cover, while the dominant shrubs in low coppice in the same territory (2 plots) were cinnecord and wild sage, also with grasses as the dominant ground covers. At Grand Turk, the dominant shrubs in natural shrub/scrub (5 plots) were darling plum (2 plots), sea grape (2 plots), and varnish leaf, with dominant respective ground covers of seashore rush-grass (2 plots), borreria (2 plots), and seaside purslane. In the Grand Turk saline/upland ecotone (5 plots) dominant shrubs were buttonwood, sea ox-eye, broom-bush, and spurge (2 plots), with seashore rush-grass the dominant ground cover in all plots. At Crooked Island, in the warbler territory 900–1000 m north of the coast in saline/upland ecotone, co-dominant shrub covers were buttonwood and black mangrove with co-dominant ground covers of woody glasswort and seaside rush-grass; saltwort, seaside purslane, horse bush, and sea ox-eye were also common on the rocky salt flat with broken honeycomb limestone (Gillis and Clench, unpubl. data). At North Caicos, the vegetation in saline/upland ecotone was structurally similar to that in the Crooked Island locality since it had the same parkland appearance. At the North Caicos site, the dominant shrub was black olive, with a dominant ground cover of white-top sedge. A *Fimbristylis,* common ernodea, box briar, silver thatch palm, varnish leaf, and wild tamarind were also collected at the site (Gillis, pers. comm.) and poison wood and sea grape noted. Overall, the dominant shrub and ground covers appeared to vary widely among plots,

sites, and islands. Large sample sizes would be required to determine which species are the most frequent dominants within warbler winter territories.

DISCUSSION

From our observations (Sykes and his group also did cursory surveys of habitat on Eleuthera and to a lesser degree on Cat Island in 1986, and Clench visited 26 islands and cays looking for Kirtland's Warbler), the observations of others, and the published literature, there appears to be no shortage of winter habitat for Kirtland's Warbler in the Bahama Archipelago. The warbler population is relatively small. If one assumes about an equal number of females to the singing males counted, this comes to 1500+ adults (1995–1997 figures), plus 1000–3000 hatching-year birds, or a total of 2500–4500 individuals at the beginning of winter. The land mass of the Bahama Archipelago is 14,500 km^2. We believe it is reasonable to assume that at least a third of the land mass offers suitable habitat, resulting in about 4829 km^2 or 1.1–1.9 km^2 available per individual. This crude estimate of the amount of winter habitat suggests that it is more than adequate for the population at present and allows for a considerable increase.

During winter, the warblers appear to be widely dispersed throughout the islands. Since the turn of the century, each of the few sightings have been of only one or two birds, despite extensive searches. There seems to be no concentration of the warblers in the archipelago, a theory investigated and then discarded by Clench after visiting 22 islands by boat from 26 February to 4 April 1976; most islands were off the usual tourist track and included five that were uninhabited: Green Cay on the edge of the Tongue of the Ocean, Little San Salvador between Eleuthera and Cat islands, Conception Island, West Plana (French) Cay between Acklins and Mayaguana, and Little Inagua (Clench 1977). No Kirtland's Warblers were found. This probable wide dispersion is also strongly supported by the fact that D. W. Buden spent eight years conducting field work mostly in the southern Bahamas and Turks and Caicos and never saw a Kirtland's Warbler. With this lack of concentration, the population should be buffered to some degree from negative factors such as droughts, severe storms, habitat losses, and predation. For example, annual rainfall is highly variable (Sealey 1994; Sykes, pers. obs.). Drought on a given island or group of islands may greatly reduce local food abundance and availability, but would not affect the entire archipelago. Consequently, at least some warblers would not be affected by such conditions. In a few places such as Abaco, free-roaming house cats (*Felis domestica*) may be a problem (R. S. Gnam, pers. comm.).

Wintering Kirtland's Warblers probably use nearly all upland habitats except high coppice within the Bahama Archipelago. Available data are not sufficient to show absolute preference for natural and secondary shrub/scrub, low coppice, and saline/upland ecotone; however, use of these four habitats comprises the majority of the observations to date.

Kirtland's Warbler in winter is clearly a bird attracted to low vegetation in the habitats in which it occurs. Since most of the upland habitats in the archipelago are structurally shrubby, that explains, at least in part, the broad use of upland habitats. Cory (1879), who collected the first specimen on Andros Island on 9 January 1879, said the bird seemed to prefer thick brush. C. J. Maynard (1896) collected 33 specimens, in or near Nassau, New Providence, and five on Eleuthera between 1884 and 1915, a period of high Kirtland's Warbler population. Maynard stated that the warblers inhabit low scrub, preferring scrub only 1–1.3 m high; with one or two exceptions, he always found the birds singly and in old fields grown up to low shrubbery (Mayfield 1996). Similarly, the site near Governor's Harbour on Eleuthera, where we studied the two individuals, had been cleared and then overgrown with shrubby vegetation. With the land use history of the Bahamas, overgrown old fields are very common. The sites on Crooked Island (Radabaugh 1974), North Caicos (Clench 1978), and Grand Turk (this study) were not old fields but natural clearings with shrub communities. A specimen taken by Paulson (1966) on San Salvador on 27 December 1963 was at the edge of scrub forest or low coppice with a 2.4–3 m canopy, having been flushed from an adjacent old field. Mayfield (1972), in his assessment of winter habitats for the

Kirtland's Warbler, concluded that the species inhabits low broad-leaved scrub, and that cleared areas allowed to grow back but that have not yet reached their maximum height and density may hold particular promise. This statement, however, was made before the birds were found in saline/upland ecotone on Crooked Island, North Caicos, and Grand Turk.

On the breeding grounds the warbler is restricted to young jack pine (*Pinus banksiana*) habitat early in the sere (usually 6–20 years of age). On the wintering grounds, a similar situation is created by the widespread subsistence agricultural practice of slash-and-burn of relatively small farms (generally 4 ha or less). Because money is seldom available for fertilizer, the nutrients are depleted from these farm plots within several years and the roughly cleared land is abandoned and reverts to upland habitat. In the course of this succession, the shrubs and trees regrow, creating habitat for the warbler. Depending on conditions, a given site may remain in a shrub stage or eventually become coppice. In the early seral stages, wild sage is often one of the most common plants. This plant produces abundant small berries that are one of the most heavily used winter foods of the Kirtland's Warbler in the northern Bahamas (Sykes, unpubl. data). Wild sage is also common in the southern Bahamas, but it seldom occurs in the saline-upland ecotone which has other shrubby plant species.

Even in the pinelands, the understory consists of a shrub layer, and it is the shrub layer the warblers are using rather than the pines. This was first mentioned by Mayfield (1992, 1996), and our observations lead us to agree. Lee and coworkers (1997) also believe that wintering Kirtland's Warblers primarily use scrub/shrub habitat, but they conclude that the species depends almost entirely on pinelands. In light of the number of old and modern records in natural habitats on non-pine islands, we cannot agree with their statement, "Prior to pre-colonial deforestation we suspect that there was little to no habitat for this bird on Eleuthera or most other non-pine islands" (Lee et al. 1997:28). Most sightings in the pinelands of Grand Bahama and the Abacos also have been compromised by frequent confusion among many observers between winter-plumaged Kirtland's Warbler and the similar plumage of the endemic race of the Yellow-throated Warbler (*Dendroica dominica flavescens*) which is quite different in appearance from the three continental races of *D. dominica* (White 1996; Sykes and Kepler, unpubl. data). Apparently, most visitors to the northern Bahamas have been unaware of the existence of the *D. d. flavescens* race of the Yellow-throated Warbler, with its yellow underparts (except for white undertail coverts) and dark streaking on the sides, because it was not adequately described or pictured in any of the popular field guides up until about 1994.

In conclusion, Kirtland's Warbler uses most of the upland habitats in the Bahama Archipelago, except high coppice, that have a shrub/scrub component with patchy small openings and openings within the vegetation at ground level. Such conditions are abundant in relatively large tracts and are widespread in the islands. Any future studies of habitat or other aspects of the species' biology during the winter period should consider using a tape recording to locate the warblers. From September through March, one might try using a tape of the call notes, and late March through April, call notes in combination with the primary song. All habitats should be searched with uniform effort.

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APPENDIX. Alphabetical listing of plants mentioned: common name, scientific and family names, growth form, status, and height. Common, scientific, and family names follow Correll and Correll (1982).

Common name	Scientific name	Family	Growth form[a]	Status[b]	Max. ht. (m)
Auricled green-brier	*Smilax auriculata*	Smilacaceae	V	N	—
Australian pine	*Casuarina equisetifolia*	Casuarinaceae	T	I	20
Avocado	*Persea americana*	Lauraceae	T	I	4.6
Banana	*Musa sapientum*	Musaceae	T	I	15
Bastard stopper	*Petitia domingensis*	Verbenaceae	T	N	20
Beef-bush	*Tabebuia bahamensis*	Bignoniaceae	S or T	N	10
Bitter bush	*Picramnia pentandra*	Simaroubaceae	S or T	N	10
Black bead	*Pithecellobium keyense*	Leguminosae	S	N	2
Black ebony	*Pera bumeliifolia*	Euphorbiaceae	T	N	12
Black-headed sedge	*Schoenus nigricans*	Cyperaceae	Se	N	0.6
Black mangrove	*Avicennia germinans*	Avicenniaceae	S or T	N	10
Black olive	*Bucida buceras*	Combretaceae	S or T	N	25
Black torch	*Erithalis fruticosa*	Rubiaceae	S or T	N	6
Bonita	*Bonita daphnoides*	Myoporaceae	S or T	N	9
Borreria	*Borreria verticillata*	Rubiaceae	PS or S	N	1
Bougainvillea	*Bougainvillea* spp.	Nyctaginaceae	V	I	4.6
Box briar	*Randia aculeata*	Rubiaceae	S	N	3
Broom-bush	*Baccharis dioica*	Asteraceae	S	N	3
Broom sedge	*Andropogon virginicus*	Gramineae	PG	N	1
Buttonwood	*Conocarpus erectus*	Combretaceae	S or T	N	20
Cabbage palm	*Sabal palmetto*	Palmae	T	N	15
Candle-berry	*Byrsonima lucida*	Malpighiaceae	S or T	N	8
Caribbean pine	*Pinus caribaea*	Pinaceae	T	N	30
Cassia	*Cassia lucayana*	Leguminosae	S	N	1.5
Cat's claw	*Pithecellobium unguis-cati*	Leguminosae	S or T	N	8
Chinese hibiscus	*Hibiscus rosa-sinensis*	Malvaceae	S	I	6
Cinnecord	*Acacia choriophylla*	Leguminosae	T	N	9
Cocobey	*Cordia bahamensis*	Boraginaceae	S or T	N	4
Coco plum	*Chrysobalanus icaco*	Chrysobalanaceae	S or T	N	6
Common ernodea	*Ernodea littoralis*	Rubiaceae	S	N	1
Common oleander	*Nerium oleander*	Apocynaceae	S or T	I	5
Copper leaf	*Acalypha wilkesiana*	Euphorbiaceae	S	I	4.6
Cow-bush	*Helicteres jamaicensis*	Sterculiaceae	S or T	N	6
Crabwood	*Ateramnus lucidus*	Euphorbiaceae	S or T	N	10
Croton	*Codiaeum variegatum*	Euphorbiaceae	S	I	3
Darling plum	*Reynosia septentrionalis*	Rhamnaceae	S or T	N	9
Fimbristylis	*Fimbristylis spathacea*	Cyperaceae	Se	N	0.5
Finger-grass	*Eustachys petraea*	Gramineae	PG	N	1.2
Frangipani	*Plumeria rubra*	Apocynaceae	T	I	8
Gumbo-limbo	*Bursera simaruba*	Burseraceae	T	N	15
Horse bush	*Gundlachia corymbosa*	Asteraceae	S	N	1.8
Ixora	*Ixora coccinea*	Rubiaceae	S	I	4.6
Japanese pittosporum	*Pittosporum tobira*	Pittosporaceae	S	I	3.7
Joe-wood	*Jacquiana keyensis*	Theophrastaceae	S or T	N	6
Jumbie bean	*Leucaena leucocephala*	Leguminosae	S or T	N	8
Lignum vitae	*Guaiacum officinale*	Zygophyllaceae	T	N	8
Logwood	*Haematoxylum campechianum*	Leguminosae	T	N	8
Mahogany	*Swietenia mahagoni*	Meliaceae	T	N	25
Maiden bush	*Savia bahamensis*	Euphorbiaceae	S or T	N	5
Mango	*Mangifera indica*	Anacardiaceae	T	I	15
Mangrove swamp vine	*Rhabdadenia biflora*	Apocynaceae	V	N	—
Morning glory	*Ipomoea indica*	Convolvulaceae	V	N	—
Myrsine	*Myrsine floridana*	Myrsinaceae	S or T	N	6
Narrow-leaved blolly	*Guapira discolor*	Nyctaginaceae	S or T	N	6
Natal-plum	*Carissa grandiflora*	Apocynaceae	S	I	5.5
Norfolk Island pine	*Araucaria excelsa*	Araucariaceae	T	I	18
Orange-jessamine	*Murraya paniculata*	Rutaceae	S or T	I	4.6

APPENDIX. Continued.

Common name	Scientific name	Family	Growth form[a]	Status[b]	Max. ht. (m)
Orchid-tree	*Bauhinia variegata*	Leguminosae	T	I	6
Pigeonberry	*Duranta repens*	Verbenaceae	S or T	N	6
Pigeon plum	*Coccoloba diversifolia*	Polygonaceae	S or T	N	7
Poison wood	*Metopium toxiferum*	Anacardiaceae	T	N	14
Powder-puff	*Calliandra haematocephala*	Leguminosae	S	I	4.6
Prickly green-brier	*Smilax havanensis*	Smilacaceae	V	N	—
Princewood	*Exostema caribaeum*	Rubiaceae	S or T	N	8
Quicksilver-bush	*Thouinia discolor*	Sapindaceae	S or T	N	5
Rat-wood	*Erythroxylum rotundifolium*	Erythroxylaceae	S or T	N	8
Red periwinkle	*Catharanthus roseus*	Apocynaceae	H	I	1
Royal poinciana	*Delonix regia*	Leguminosae	T	I	12
St. Andrew's cross	*Hypericum hypericoides*	Guttiferae	S	N	1
Saltwort	*Batis maritima*	Bataceae	S	N	0.6
Scarlet sage	*Salvia splendens*	Labiatae	H	I	0.4
Sea grape	*Coccoloba uvifera*	Polygonaceae	S or T	N	15
Sea ox-eye	*Borrichia arborescens*	Asteraceae	S	N	1
Seashore rush-grass	*Sporobolus virginicus*	Gramineae	PG	N	0.2
Seaside purslane	*Sesuvium portulacastrum*	Aizoaceae	PH	N	0.1
Short-leaved wild fig	*Ficus citrifolia*	Moraceae	S or T	N	15
Silver thatch palm	*Coccothrinax argentata*	Palmae	T	N	10
Slender nut-rush	*Scleria lithosperma*	Cyperaceae	Se	N	0.6
Small-flowered prickly apple	*Catesbaea parviflora*	Rubiaceae	S	N	2
Smooth passion-flower	*Passiflora cupraea*	Passifloraceae	V	N	—
Soap-berry	*Exothea paniculata*	Sapindaceae	S or T	N	20
Soldier-bush	*Tournefortia volubilis*	Boraginaceae	V	N	—
Southern bracken fern	*Pteridium aquilinum*	Polypodiaceae	F	N	3
Spanish stopper	*Eugenia foetida*	Myrtaceae	T	N	6
Spreading torch	*Erithalis diffusa*	Rubiaceae	S	N	1.5
Spurge	*Euphorbia abbreviata*	Euphorbiaceae	S	N	0.5
Strangler fig	*Ficus aurea*	Moraceae	T	N	20
Strong-back	*Bourreria ovata*	Boraginaceae	S or T	N	10
Strong back	*Krugiodendron ferreum*	Rhamnaceae	S or T	N	10
Sweet torchwood	*Nectandra coriacea*	Lauraceae	T	N	12
Tetrazygia	*Tetrazygia bicolor*	Melastomataceae	S or T	N	6
Torchwood	*Amyris elemifera*	Rutaceae	S or T	N	5
Touch-me-not	*Malpighia polytricha*	Malpighiaceae	S	N	3
Trailing wedelia	*Wedelia trilobata*	Asteraceae	PH	I	0.2
Varnish leaf	*Dodonaea ehrenbergii*	Sapindaceae	S or T	N	5
Vernonia	*Vernonia bahamensis*	Asteraceae	PS	N	1.5
Weeping bottlebrush	*Callistemon* spp.	Myrtaceae	S or T	I	6
West Indian snowberry	*Chiococca alba*	Rubiaceae	S	N	3
White ironwood	*Hypelate trifoliata*	Sapindaceae	T	N	13
White stopper	*Eugenia axillaris*	Myrtaceae	S or T	N	8
White-top sedge	*Dichromena colorata*	Cyperaceae	Se	N	0.5
Whitewood	*Drypetes diversifolia*	Euphorbiaceae	T	N	7
Wild cassada	*Bumelia salicifolia*	Sapotaceae	T	N	16
Wild cotton	*Gossypium hirsutum*	Malvaceae	H or S	I	4
Wild dilly	*Manilkara bahamensis*	Sapotaceae	T	N	10
Wild guava	*Psidium longipes*	Myrtaceae	S or T	N	4
Wild lime	*Zanthoxylum fagara*	Rutaceae	S or T	N	10
Wild saffron	*Bumelia americana*	Sapotaceae	S or T	N	13
Wild sage	*Lantana involucrata*	Verbenaceae	S	N	2
Wild tamarind	*Lysiloma latisiliquum*	Leguminosae	T	N	16
Wild yam	*Rajania hastata*	Dioscoreaceae	V	N	—
Woody glasswort	*Salicornia virginica*	Chenopodiaceae	PH	N	0.25
Woolly corchorus	*Corchorus hirsutus*	Tiliaceae	S	N	2
Yellow alder	*Turnera ulmifolia*	Turneraceae	H or S	N	1

[a] F = fern, G = grass, H = herb, P = perennial, S = shrub, Se = sedge, T = tree, V = vine.
[b] I = introduced non-native species, N = native species.

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NESTING BIOLOGY OF THE BAIRD'S SPARROW IN SOUTHWESTERN MANITOBA

STEPHEN K. DAVIS[1,2,3] AND SPENCER G. SEALY[1]

ABSTRACT.—Very few studies have documented aspects of Baird's Sparrow (*Ammodramus bairdii*) nesting biology, apparently because of difficulty in locating their nests. Subsequently much of the information regarding the breeding biology of the Baird's Sparrow is based on small samples of nests and anecdotal information. We studied the nesting biology of the Baird's Sparrow in southwestern Manitoba, during 1991–1992. Baird's Sparrows arrived in the first two weeks of May and initiated clutches as early as 25 May. Clutch initiation peaked between 29 May and 4 June with a second smaller peak occurring in mid- to late July. Seventy-six nests were located with a mean clutch size of 4.6 eggs. The incubation period extended 11–12 days and young fledged between 8 and 11 days of age. Mayfield nest success was 37% with predation being the primary cause of nest loss. Brown-headed Cowbirds (*Molothrus ater*) parasitized 36% of the nests with 67% of these nests containing more than one cowbird egg ($\bar{x}$ = 2.0 ± 0.2 S.E., range = 1–4). Hatching success of non-parasitized nests was significantly higher than that of parasitized nests. In addition, significantly fewer young fledged from successful parasitized nests than from successful non-parasitized nests resulting in an average cost of 1.1 Baird's Sparrow fledglings per parasitized nest. Egg removal by cowbirds was likely the primary cause of lowered productivity in parasitized nests. Baird's Sparrows appear to be a good quality host for cowbirds in southwestern Manitoba as 21% of cowbird eggs laid fledged young with 0.5 cowbirds fledging per parasitized nest. *Received 15 Aug. 1997, accepted 13 Jan. 1998.*

The Baird's Sparrow (*Ammodramus bairdii*) is endemic to the grasslands of the northern Great Plains (Knopf 1994), breeding from northern South Dakota north to southern Alberta, Saskatchewan and southwestern Manitoba (Rising 1996). This species was once considered one of the most common birds on the Manitoba prairies (Thompson 1891), but with a decline of more than 95% of the native mixed-grass prairie in Manitoba (R. E. Jones, pers. comm.), its range is now restricted to fragments of habitat in extreme southwestern Manitoba (Rising 1996). In 1989, the Baird's Sparrow was listed as "threatened" by the Committee On the Status of Endangered Wildlife in Canada (COSEWIC; Goossen et al. 1993), but was subsequently delisted in 1996 (COSEWIC 1996). The Baird's Sparrow is currently listed as an endangered species in Manitoba.

Early studies suggested that the Baird's Sparrow was a native prairie specialist (Cartwright et al. 1937, Owens and Myres 1973), although more recent studies indicate that the species is more flexible in its habitat choice than previously thought. Indeed, the species has been recorded in other habitat types such as seeded pasture, hayland, and cropland (reviewed by Davis et al. 1996). Several studies have focused on habitat requirements of Baird's Sparrows (Dale 1983, Sousa and McDonal 1983, Mahon 1995, Sutter et al. 1995, Davis and Duncan in press) and the effects of different land management practices such as fire, grazing, and haying on the species (Owens and Myres 1973, Kantrud and Kologiski 1982, Dale 1984, Renken and Dinsmore 1987, Pylpec 1991, Winter 1994, Madden 1996). Only one study has documented aspects of the species' nesting biology, apparently because of difficulty in locating their nests (Cartwright et al. 1937, Lane 1968). Subsequently much of the information regarding the breeding biology of the Baird's Sparrow is based on small samples of nests (Cartwright et al. 1937) and anecdotal information.

The objectives of this study were to: (1) examine nesting biology parameters such as egg, nest and clutch size, phenology of clutch initiation, nest construction, timing of egg laying, and length of incubation and nestling periods; (2) quantify nesting success; (3) examine factors influencing nest predation and its effect on nesting success; and (4) determine the frequency and effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Baird's Sparrow productivity.

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STUDY AREA AND METHODS

Field work was conducted from 6 May to 17 August 1991 and 1 May to 25 August 1992 on four typical grassland sites in southwestern Manitoba. Site 1 (49° 04′ N, 101° 14′ W) was a square, 64-ha patch of idle hayland comprised predominantly of smooth brome grass (*Bromus inermis*), along with *Stipa spartea, Poa* spp., *Koeleria gracilis,* and *Artemisia frigida.* Site 2 (49° 24′ N, 101° 02′ W) was a square, 64-ha patch of grazed, gently rolling pasture with numerous depressions. Low areas were characterized by *Calamagrostis inexpansa* and sedges (*Carex* spp.), whereas *Agropyron repens, S. spartea* and *Bouteloua gracilis* were predominant on elevated areas. Western snowberry (*Symphoricarpos occidentalis*) and wolf willow (*Eleagnus commutata*) occurred in patches throughout. Site 3 (49° 30′ N, 100° 56′ W) was an irregular-shaped 22-ha strip of native grassland characterized by *S. spartea, Muhlenbergia richardsonis,* and *B. gracilis* and bordered by stands of wolf willow, western snowberry, and *Salix* spp. Although this site was periodically grazed in the past, no cattle were present on the site in 1991 and 1992 (see Davis 1994, Davis and Sealy, in press, for more detailed descriptions of sites 1–3). Site 4 (49° 04′ N, 101° 17′ W) was an irregularly-shaped 20-ha strip of native grassland, comprised of *S. spartea, M. richardsonis,* and *Deschampsia caespitosa.* The site was last hayed in 1990 and was included in the study only in 1991 because of the landowner's intent to hay in 1992.

Each site was marked in a 50-m grid with labelled surveyor flags positioned as close to the top of the vegetation as possible. Baird's Sparrows and Brown-headed Cowbirds were not observed perching on the flags during the course of this study.

Female Baird's Sparrows were flushed from their nests by two persons dragging a weighted 30-m nylon rope with aluminum and tin cans attached every 0.5 m. Each plot was entirely and systematically dragged throughout the field season. To reduce the chances of human-induced nest failure, nest-searches were not conducted during cold, wet weather. Nest-searching commenced each year in the second week of May and finished in the first week of August. Nests were marked with surveyor flags 5 m away and were inspected every 2–4 days until the young fledged or the nesting attempt ended. Because research activities may influence predation rates of ground-nesting birds (Major 1990, but see O'Grady et al. 1996) we took several precautions when checking nests. Before approaching the nest site, we checked the area for potential nest predators and cowbirds. To avoid creating a well-defined path, we approached nests from different directions and attempted to stay about 1 m away when inspecting their contents. Nests were considered successful if at least one nestling (host or cowbird) survived to fledging age. Cues used to determine whether empty nests were successful included a combination of the condition of the nest (i.e., compacted, but not disrupted) and the presence of an adult carrying food or uttering alarm calls nearby. Nest success was evaluated by calculating daily survival rates derived from the incubation and nestling stages (Mayfield 1975). In addition, the proportions of successful and unsuccessful nests are presented for comparison with previous studies which did not use the Mayfield method of calculating nest success.

Clutch initiation dates were calculated for nests found during egg laying by back-dating at a rate of 1 egg laid per day (see below). For other nests, clutch initiation dates were estimated by subtracting the length of the incubation period and the size of the completed clutch from the day hatching began. Clutches were considered complete when the number of eggs was the same for two successive days. The clutch size of Baird's Sparrows was determined from non-parasitized nests and parasitized nests in which the final number of host eggs laid was known. In comparisons of clutch size in parasitized and non-parasitized nests, the clutch size of parasitized nests was defined as the number of host eggs remaining in the nest after host and cowbird laying was complete. Wilcoxon rank sum was used to compare mean clutch size, eggs hatched, and young fledged in parasitized and non-parasitized nests. Nests parasitized during the nestling period or after the nest was terminated were treated as non-parasitized for the above comparisons because cowbirds could not have affected host clutch sizes.

Inside diameter and depth of nests with eggs, and length and width of eggs were measured with calipers to the nearest 0.1 mm. Nest concealment was determined in 1992 only, by using a circular, 6.3-cm-diameter piece of white plastic divided into 8 equal black-and-white sections. The disc was placed horizontally into each nest after nest measurements were taken and the number of visible sections was recorded from 1 m away at five points (each cardinal direction and overhead). Completely exposed nests, therefore, had a value of 40, whereas completely concealed nests were 0. Nest concealment was assessed on sunny days, 5–6 h after sunrise and were only assessed on nests containing eggs or newly hatched young.

A measuring wheel was used to measure the distance of each nest to the nearest perch site after the nesting attempt had ended. Perch sites were defined as any object (e.g., shrub, fence, rock pile, etc.) that was at least 1 m in height (Gochfeld 1979) and could support a cowbird. Distances between nest sites and nearest perches were log-transformed to meet the assumption of normality. Data were lumped if no significant differences were detected between years ($a = 0.05$). Means are presented with standard errors. All analyses were performed using SAS (ver. 6) statistical software.

We also present nesting biology data on Baird's Sparrows from records in the Canadian Prairie Nest Record Scheme (PNRS) for comparative purposes. The Canadian PNRS is a collection of nest records from species nesting in Manitoba, Saskatchewan, and Alberta.

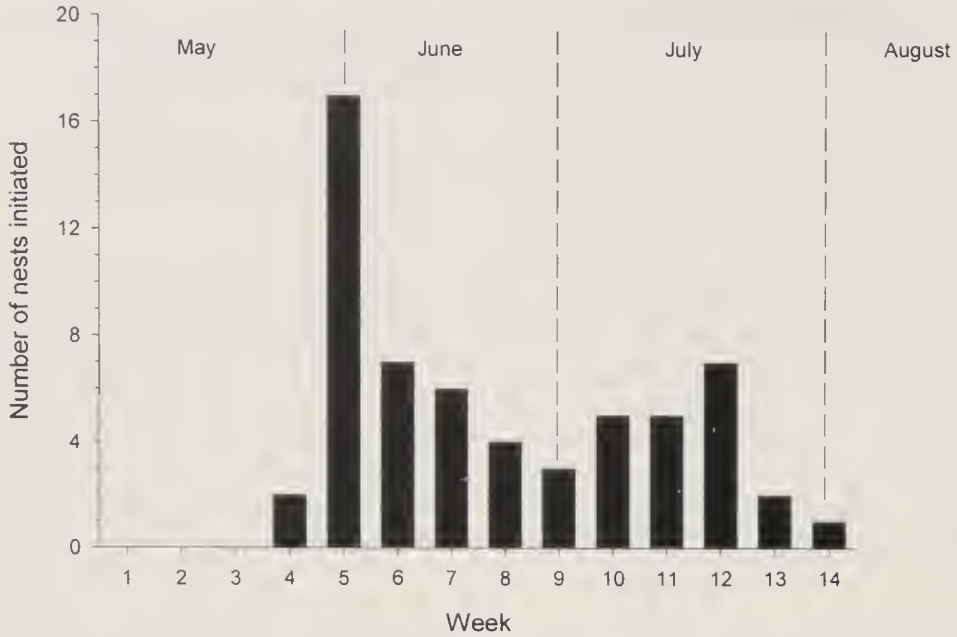

FIG. 1. Frequency distribution of Baird's Sparrow clutch initiation dates in southwestern Manitoba (n = 59 nests). Week 1 = 1–7 May, Week 2 = 8–14 May, Week 3 = 15–21 May, Week 4 = 22–28 May, Week 5 = 29 May–4 June, Week 6 = 5–11 June, Week 7 = 12–18 June, Week 8 = 19–25 June, Week 9 = 26 June–2 July, Week 10 = 3–9 July, Week 11 = 10–16 July, Week 12 = 17–23 July, Week 13 = 24–30 July, Week 14 = 31 July–6 August.

RESULTS AND DISCUSSION

Nesting biology.—The first Baird's Sparrow was recorded on the study area on 10 May 1991 and 4 May 1992, consistent with arrival times recorded in other areas. Belcher (1980), for example, stated that the species usually arrives in south-central Saskatchewan in the second week of May but may be as early as 4 May. In comparison, Baird's Sparrows typically arrive in Alberta in the third week of May (Semenchuk 1992).

Seventy-six nests were located over the two years of the study. Clutch initiation peaked 29 May–4 June with an apparent second, smaller peak in mid- to late July (Fig. 1). The median clutch initiation date was 16 June with the earliest and latest clutches initiated 25 May and 31 July, respectively. Although data from the PNRS (n = 33 nests) revealed that the length of the laying season was the same as in this study, the median clutch initiation date (10 July) was much later. These records, however, were not systematic nest searches conducted throughout the nesting season as in this study, and might reflect a bias towards individuals locating nests later in the season (see below). The nesting season in North Dakota (Stewart 1975) appears similar to what we found with egg dates ranging from 5 June to 21 July for 23 nests examined. In contrast, Cartwright et al. (1937) reported that laying did not begin until mid-June in Manitoba, and Lane (1968) believed that Baird's Sparrows delayed their nesting until late June. In these studies it is unclear as to when the authors initiated nest searches or on how many nests they based their conclusions.

TABLE 1. Timing of egg laying in two Baird's Sparrow nests in southwestern Manitoba.

Nest no.	Egg no.	Laying interval (CST)
37	2	05:13–06:12
37	3	05:18–06:33
37	4	06:41–07:42
140	3	05:35–07:30

Baird's Sparrows lay one egg per day in the early morning between 05:13 and 07:42 Central Standard Time (CST; Table 1). These laying times are consistent with those found for other grassland songbirds. On 27 and 28 May, 1992, we recorded a Western Meadowlark (*Sturnella neglecta*) laying its fourth egg between 06:19 and 07:10 CST, and its fifth egg between 07:20 and 08:09 CST. Chestnut-collared Longspurs (*Calcarius ornatus*) have been recorded laying their eggs between 06:00 and 07:30 CST (Hill and Gould 1997).

The mean size of 251 Baird's Sparrow eggs

TABLE 2. Distribution of Baird's Sparrow clutch sizes (n = 61) in relation to the median clutch initiation date, 16 June.

Clutch size	3	4	5	6
Occurrence (%)	1.6	36.1	60.7	1.6
Before median date (%)	0	50	73	100
After median date (%)	100	50	27	0

was 19.3 ± 0.1 mm long by 14.7 ± 0.0 mm wide with a range of 17.0–21.3 mm long and 13.3–15.6 mm wide. These measurements fall within the range of those given for 18 and 50 eggs by Cartwright et al. (1937) and Lane (1968), respectively.

Mean clutch size was 4.6 ± 0.1 eggs (n = 61) in this study and 4.5 ± 0.1 eggs (n = 24) from the PNRS, similar to that found in North Dakota (n = 15 nests, $\bar{x}$ = 4.7 eggs; Stewart 1975). Clutch sizes in southwestern Manitoba ranged from 3 to 6 eggs with 5-egg clutches being the most common (Table 2). This supports Cartwright's and coworkers' (1937) claim that 5 eggs is the typical clutch size for Baird's Sparrow, although 4-egg clutches occur frequently. Most 5-egg clutches (73%) were initiated before the median clutch initiation date (Table 2) resulting in significantly larger clutches (4.8 ± 0.1) being initiated prior to the median initiation date compared to later dates (4.4 ± 0.1; Wilcoxon rank sum: U = 2.16, P = 0.031). Smaller clutches later in the season may have resulted from reduced metabolic resources as a result of re-nesting and double brooding (Wray et al. 1982), although factors such as age and cost of reproduction may also be involved (reviewed by Rohwer 1992).

Cartwright and coworkers (1937) stated that Baird's Sparrow nests are always placed on the ground amongst grasses and are either: (1) in a tuft of grass supported by a shrub, (2) in a depression beneath an overhanging tuft of grass, or (3) in a deep depression with no overhead concealment. The latter two types more accurately describe nests in this study as 61% of the nests were in depressions situated at the base or within clumps of dead and live narrow-leaf grasses (< 5 mm wide). Twenty-three percent and 16% of the nests were associated with *B. inermis* and *A. frigida*, respectively. *Artemisia frigida* stems were incorporated into the outer lining of those nests built next to it. Nests not associated with *A. frigida* had an outer lining constructed of grass stems and leaves, and an inner lining of fine narrow-leaf grasses and rootlets, similar to that described by Lane (1968). Occasionally bailing twine, cow hair, and red setae from moss were incorporated into the inner lining. None of the nests was directly associated with shrubs in this study despite their occurrence on the sites. However, Baird's Sparrow nests have been found at the base of young western snowberry shrubs (< 40 cm) in native pastures of southern Saskatchewan (Davis, unpubl. data).

Inside dimensions of nests averaged 6.2 ± 0.1 cm in diameter and 4.6 ± 0.1 cm in depth (n = 64 nests), consistent with the inside dimensions reported by Cartwright and coworkers (1937; 6.4 cm diameter and 3.8 cm deep). No significant differences were found for nest diameter and nest depth before and after the median clutch initiation date (Student's t-test: t = 0.741 and t = 0.631, respectively, $P > 0.05$ for both). Thus Baird's Sparrows did not appear to alter nest size in response to warmer temperatures later in the summer, as reported for Western Meadowlarks (Dickinson et al. 1987)

The incubation period of three clutches for which laying and hatching dates were known, ranged from 11–12 days from the last egg laid to the last egg hatched. Lane (1968) found that two Baird's Sparrow nests were also incubated for 11–12 days. Baird's Sparrow young fledged between 8 and 11 days after hatching in 23 nests in which the fledging dates could be determined (see also Cartwright et al. 1937). Allowing five days for laying, 11–12 days for incubation and 8–11 days to fledging, one nesting attempt would take 24–28 days to complete (excluding nest-building time). Because the laying season for Baird's Sparrow is approximately 70 days in Manitoba, sufficient time is available to raise more than one brood. Indeed, we recorded one instance of a Baird's Sparrow producing a second brood. A banded female fledged young at one nest between 13 and 15 July and was recaptured 50 m north at a second nest that she initiated on 20 or 21 July. Thus 5–8 days elapsed from the fledging of the first brood to the initiation of the second nest. Indirect evidence of possible double-

TABLE 3. Baird's Sparrow nest success and productivity in southwestern Manitoba (MB) and from the Canadian Prairie Nest Record Scheme (PNRS).

	MB (n = 74 nests)	PNRS (n = 34 nests)
Incubation daily survival rate	0.958	0.953
Nestling daily survival rate	0.948	0.939
Mayfield nest success	0.37	0.32
% Successful	54	44
% Depredated	39	47
% Deserted	3	9
% Failed	4	0
Young fledged/nest ($\bar{x}$ ± SE)	1.4 ± 0.2	1.7 ± 0.3
Young fledged/successful nest ($\bar{x}$ ± SE)	2.8 ± 0.2	3.8 ± 0.3
% Eggs laid that fledged young (n)[a]	35 (285)	20 (87)
% Eggs incubated to full term that fledged young (n)[a]	43 (232)	48 (21)

[a] Number of eggs.

brooding is also suggested by the apparent second peak in clutch initiation (Fig. 1). Cartwright and coworkers (1937) suspected that 3 of 5 observed pairs successfully raised two broods and stated that the second nests were initiated no later than one day after the fledging of young from the first. There was, however, no indication that the authors had marked birds to substantiate their claim.

Nest success.—Of 74 nests in which the nest fate was known, 54% fledged at least one young (Table 3), comparable to other ground-nesting passerines in the area (Davis 1994). Predation was the primary cause of nest loss in this study and for those nests recorded in the PNRS (Table 3). Nests initiated earlier in the breeding season were as likely to be depredated as nests initiated later in the season as the proportion of nests depredated before the median clutch initiation date (44%) was similar to those initiated after this date (31%; χ^2 = 1.192, df = 1, $P > 0.05$). Nest desertion and failure not related to predation were not important factors influencing nest success. In our study, cattle trampled one nest, whereas inclement weather was believed to be responsible for the death of young in another nest, and a third nest with young failed for an unknown reason. Mayfield nest success on our study was 37% (Table 3). Daily survival rates were similar for the nestling and incubation stages in this study and for 34 nests from the PNRS in which Mayfield nest success could be calculated. Overall, a mean of 1.4 ± 0.2 young fledged per nest while successful nests fledged an average of 2.8 ± 0.2 young per nest (Table 3). Baird's Sparrow young fledged from 35% of the total number of eggs laid, and from 43% of the eggs incubated to full term in this study. Data from the PNRS indicate that 20% of the eggs laid and 48% of the eggs incubated to full term fledged young (Table 3).

Nests were situated an average of 72.5 ± 7.6 m (range = 6–365 m) from the nearest perch that was at least 1 m in height. Proximity to perches did not influence nest predation as the mean perch distance to depredated nests (70.1 ± 10.6 m) was not significantly different from those nests that were not depredated (70.8 ± 10.8 m; Student's t-test: $t = 0.095$, $P > 0.05$). Nest concealment also did not influence predation as no significant differences in concealment values were found for depredated (13.1 ± 1.5) and successful nests (9.6 ± 1.5; Student's t-test: $t = 1.587$, $P > 0.05$). The lack of relationship between nest concealment or perch distance with predation frequency suggest that birds were not the primary nest predators because avian nest predators often hunt from perches (Preston 1957) and rely on visual cues when foraging. Avian predators should, therefore, be influenced more by nest concealment than mammalian or reptilian predators (Clark and Nudds 1990). In fact, striped skunk (*Mephitis mephitis*) and thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) likely depredated two nests as fresh skunk scat was located next to one depredated nest and another depredated nest was built over a thirteen-lined ground squirrel burrow. Other potential predators frequently observed on the study sites were: American Crow (*Corvus brachyrhyncos*), Northern Harrier (*Circus cyaneus*), western plains garter snake (*Thamnophis radix haydeni*), and Richardson's ground squirrel (*Spermophilus richardsonis*).

Cowbird parasitism.—Brown-headed Cowbirds parasitized 36% of Baird's Sparrow nests on our study area and laid 2.0 ± 0.2 eggs in parasitized nests (Table 4). More than

TABLE 4. Parasitism frequency and cowbird productivity in Baird's Sparrow nests from southwestern Manitoba (MB) and the Canadian Prairie Nest Record Scheme (PNRS).

	MB	PNRS
% Nests parasitized (n)	36 (74)	11 (27)
% Multiple parasitism (n)	67 (27)	100 (3)
% Cowbirds fledged from eggs laid (n)	21 (56)	29 (7)
Cowbird eggs laid/parasitized nest ($\bar{x} \pm$ SE)	2.0 ± 0.2	2.3 ± 0.3
Cowbird young fledged/parasitized nest ($\bar{x} \pm$ SE)	0.5 ± 0.1	0.7 ± 0.7

TABLE 5. Distribution of cowbird eggs laid in Baird's Sparrow nests in southwestern Manitoba (MB) and the Canadian Prairie Nest Record Scheme (PNRS).

No. of cowbird eggs laid	% Nests in MB (n)	% Nests in PNRS (n)
1	33 (9)	—
2	41 (11)	66 (2)
3	22 (6)	33 (1)
4	4 (1)	—

one cowbird egg was laid in 67% of parasitized nests (Table 4) and most of these nests contained 2 cowbird eggs (Table 5). Of the 61 nest records in the PNRS, 27 records with sufficient information revealed that 3 nests were parasitized (Table 4) and each nest contained more than one cowbird egg (Table 5). These records are likely not a reliable indication of the frequency of parasitism in prairie Canada since 50% of the clutches in the PNRS were initiated after 10 July, which is near the end of the cowbird laying season (Davis 1994).

Insight into the extent to which Baird's Sparrows were parasitized by cowbirds in the past is also difficult to determine because so few nests have been recorded. Friedmann (1963) indicated that there were four known instances of parasitism from North Dakota, one from Manitoba, and another from an unknown locality. The latter nest was most likely from the Rush Lake area of Saskatchewan (Raine 1894). The only other record of a parasitized Baird's Sparrow nest also came from Saskatchewan (Friedmann and Kiff 1985). It is interesting to note that, as in the current study, most of the parasitized nests recorded above contained more than one cowbird egg.

Although we cannot determine whether the results of this study are typical of the frequency of cowbird parasitism on Baird's Sparrow nests throughout the range, Davis (unpubl. data) found that 32% of 61 Baird's Sparrow nests located in southern Saskatchewan were parasitized by cowbirds and that 79% of these nests contained more than one cowbird egg. Because Baird's Sparrows nest entirely within the cowbirds' laying season (Davis 1994), and accept cowbird eggs, the species is highly susceptible to cowbird parasitism and may be a more common host than previous records indicate.

This study represents the first published account of Baird's Sparrows fledging cowbirds (Friedmann 1963, Friedmann and Kiff 1985). In the PNRS, one of the three parasitized nests may also have fledged cowbird nestlings because the nest was found with two cowbird and one host young that were "ready to fledge". Baird's Sparrows appear to be good quality hosts in southwestern Manitoba as they fledged 21% of the cowbird eggs laid in their nests (Table 4). This is higher than the cowbird nest success reported by Elliott (1978) for Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*) in Kansas, but similar for Grasshopper (22%) and Savannah (*Passerculus sandwichensis*; 30%) sparrows in southwestern Manitoba (Davis and Sealy, in press).

Baird's Sparrows fledged significantly fewer young from successful parasitized nests (1.9 ± 0.4) than from successful non-parasitized nests (3.0 ± 0.3; Table 6). On average, cowbird parasitism cost Baird's Sparrows 1.1 fledglings per successful nest, similar to the cost of cowbird parasitism found in studies of other ground-nesting host species (Nice 1937, Hill 1976, Elliott 1978, Zimmerman 1983, Trail and Baptista 1993; but see Smith 1981). Of eight species examined in southwestern Manitoba, only parasitized Savannah Sparrows incurred a larger cost (2.2 young) than Baird's Sparrows (Davis and Sealy, in press). Cowbirds often lower host productivity through the removal or damage of host eggs when they parasitize nests (Sealy 1992) and when cowbird nestlings out-compete host nestlings for food and space (Rothstein 1975,

TABLE 6. Hatching success and productivity ($\bar{x} \pm$ SE) in parasitized and non-parasitized Baird's Sparrow nests in southwestern Manitoba.

	Non-parasitized (n)[a]	Parasitized (n)[a]	P[b]
Clutch size	4.5 ± 0.1 (49)	3.1 ± 0.4 (22)	<0.001
Host eggs laid that hatched	3.2 ± 0.2 (49)	2.1 ± 0.4 (22)	0.03
Host eggs incubated full term that hatched	4.1 ± 0.1 (38)	3.3 ± 0.3 (15)	0.013
Host young fledged/nest	1.4 ± 0.2 (50)	1.4 ± 0.3 (22)	>0.05
Host young fledged/successful nest	3.0 ± 0.3 (23)	1.9 ± 0.4 (16)	0.023

[a] Number of nests.
[b] Wilcoxon rank sum.

Payne 1977). Egg removal by cowbirds may have been responsible for the lower productivity in parasitized nests because parasitized nests had significantly fewer eggs per clutch than non-parasitized nests (3.1 and 4.5 egg, respectively), and fewer young hatched from eggs which were fully incubated in parasitized nests compared to non-parasitized nests (3.3 and 4.1 young, respectively; Table 6). Thus cowbirds likely removed an average of one host egg per parasitized nest, fewer than reported by Elliott (1978).

Loss and degradation of grassland habitat are believed to be important factors contributing to the consistent and widespread decline of grassland birds in North America (Peterjohn and Sauer 1993, Herkert 1994, Knopf 1994). Habitat fragmentation, for example, reduces average patch size and increases the ratio of edge to interior habitat. This may ultimately lead to reduced productivity of grassland birds because of the increased activity of nest predators and Brown-headed Cowbirds along edge habitats (Gates and Gysel 1978, Johnson and Temple 1990). Our results appear to support this contention as nest predation and cowbird parasitism reduced Baird's Sparrow productivity in this highly fragmented region of the province. However, we cannot determine the overall impact of these factors on the seasonal productivity of Baird's Sparrows in this portion of their range without information on the number of breeding attempts per season and the reduction in productivity per breeding attempt (May and Robinson 1985, Smith and Arcese 1994). Clearly, more research on the impacts of nest predation and cowbird parasitism is required to determine the demographic effects of these factors on Baird's Sparrow populations in altered and native landscapes across the sparrow's breeding range.

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AVIAN RESOURCE USE IN DOMINICAN SHADE COFFEE PLANTATIONS

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ABSTRACT.—We quantified foraging behavior of 19 bird species in shade coffee plantations in the Dominican Republic to document and evaluate their use of food resources in the shade overstory relative to the coffee understory. All species were observed foraging in the *Inga vera* overstory, and 18 of the 19 species had median foraging heights significantly above the median maximum coffee height. Eight species (42%) foraged exclusively in the canopy or subcanopy and not in the coffee understory. No species foraged exclusively in the coffee, although the Narrow-billed Tody (*Todus angustirostris)* foraged mostly in coffee. A negative correlation was found between a species' median foraging height in our shade plantations and its abundance in nearby sun coffee plantations. Invertebrates and nectar were the most important food items in the *Inga* overstory where 95% of the species gleaned leaf surfaces, 63% probed flowers, 58% gleaned or probed wood, 47% used epiphytes (for invertebrates or fruits), and 26% gleaned or probed *Inga* fruit. In contrast, birds in coffee foraged primarily for invertebrate prey as 42% of all species gleaned leaf surfaces, 21% gleaned or probed wood, 21% gleaned or probed fruit, and 5% probed flowers. The *Inga* overstory was an important foraging site for most species suggesting that plantations without a shade overstory (i.e., sun coffee) will have a lower diversity and abundance of food and hence are less attractive to birds than traditional shade plantations. *Received 5 May 1997, accepted 11 Nov. 1997.*

SINOPSIS.—Cuantificamos el comportamiento alimenticio de 19 especies de aves en plantaciones de café de sombra en la República Dominicana para documentar y evaluar el uso de estas del recurso alimenticio en el dosel en relación al sotobosque de cafetos. Todas las especies fueron observadas alimentándose en el dosel de *Inga vera*; y en 18 de las 19 especies la mediana de altura de forrajeo fue significativamente mayor a la mediana de la altura máxima del café. Ocho especies (42%) se alimentaban exclusivamente en el dosel y no en el sotobosque de café. Ninguna especie se alimentaba exclusivamente en los cafetales, aún cuando *Todus angustirostris* lo hacia primordialmente en el café. Una correlación negativa fue encontrada en la altura mediana de forrajeo y en su abundancia en nuestras plantaciones de café a la sombra y las plantaciones de café de sol cercanas. Los invertebrados y el néctar fueron las fuentes de comida más importantes en el dosel de *Inga* donde el 95% de las especies se alimentaban picoteando ("gleaning") la superficie de las hojas, el 63% probaba las flores, el 58% probaba o picoteaba la madera, el 47% usaba las epífitas (para colectar invertebrados o frutas) y el 26% probaba o picoteaba en las frutas de *Inga*. Por el contrario, las aves en el café primordialmente cazaban invertebrados, ya que el 42% picoteaban en las superficies de las hojas, el 21% picoteaban o proban las madera, el 21% picoteaban y probaban las frutas, y el 5% probaban las flores por su néctar. El dosel de *Inga* fue un importantísimo lugar de forrajeo para la mayoría de las especies, suguiriendo que las plantaciones que carezcan de un dosel con sombra (tal como el café de sol) tendrán una menor diversidad y abundancia de comida haciéndolas así menos atractivas para las aves que las plantaciones tradicionales de sombra.

Coffee plantations with a shade overstory can have an abundance of birds and provide habitat for some forest species (e.g., Wetmore 1916; Griscom 1932; Aguilar-Ortiz 1982; Beehler et al. 1987; Wunderle and Latta 1996; Greenberg et al. 1997a,b). Given the attractiveness of these agroforestry plantations for birds, Oldfield (1988) and Thiollay (1995) have suggested that such plantations could function as buffer zones for some tropical forest reserves by extending the area covered by overstory canopy. Unfortunately, the current trend in coffee cultivation is to eliminate the shade overstory as farmers convert to higher-yielding coffee grown in open sunlight (Perfecto et al. 1996). This "sun coffee" does not support forest species as often as is found in traditional shade coffee plantations (Borrero 1986, Wunderle and Latta 1996, Greenberg et al. 1997a), and requires higher inputs of fertilizers and pesticides (Greenberg 1994, Vannini 1994, Wille 1994, Rice and Ward 1996). The ecological implications of this change in coffee cultivation is especially important in northern Latin America and the Caribbean where coffee plantations cover approximately 2.7 million ha at mid-elevation sites which

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have already been extensively deforested (Rice and Ward 1996).

To encourage coffee farmers to retain their shade overstory, an effort is underway to promote the labeling of coffee packages designating a shade plantation origin (Greenberg 1994, Wille 1994, Rice et al. 1997). This labeling scheme would encourage environmentally conscientious consumers to purchase shade coffee, thereby using the marketplace to promote the maintenance of shade canopy trees in some tropical agricultural landscapes. However, before such a program is initiated, it is valuable to understand how wildlife use shade plantations and what attracts them to plantations.

Despite the potential value of shade coffee for bird populations, only Greenberg and coworkers (1997a) have quantified some aspects of resource use by birds in shade plantations. Therefore, the objective of this study is to describe where and how birds forage in shade coffee plantations to determine the food resources utilized by birds in shade coffee plantations in the Dominican Republic on the Caribbean island of Hispaniola. These observations will allow us to evaluate the importance of the shade overstory relative to the coffee understory in attracting birds to coffee plantations.

STUDY SITE AND METHODS

Fourteen shade coffee plantations (mean = 1.2 ha, range 0.1–8.7 ha) were sampled in the vicinity of Manabao (19° 6′ N, 70° 48′ W) and Jarabacoa (19° 9′ N, 70° 39′ W), La Vega province, at an altitude of 560–840 m in the Cordillera Central of the Dominican Republic. The plantations are located in a zone receiving an annual rainfall of approximately 1200 mm per year (Hartshorn et al. 1980) and classified as subtropical moist forest in the Holdridge life zone system (Anonymous 1967). One hundred meter transects run in the four major cardinal directions from each plantation (Wunderle and Latta, unpublished data) indicate that 75% of the land area surrounding the plantations is non-forest (67% pasture and 8% cultivation of low ground crops). Tree canopies cover 20% of the surrounding area (13% wooded arroyo; 5% coffee plantations; 2% pine) and the remaining 5% of the land area contains a miscellaneous mix of roads, buildings, rivers, etc.

We used 27 16-m diameter circular plots (0.02 ha) to quantify vegetation distribution in the plantations. A single plot was placed in the center of each small plantation (0.1–0.6 ha), and three to seven plots were placed at 100 m intervals in the larger plantations (2.5–8.7 ha). Within each plot we measured all stems at least 3 cm at 1.3 m from the base (DBH). Stems less than 3 cm were measured in belt transects of 1.7 m width along the four cardinal directions from the plot center. Each belt transect was sampled by walking the north, south, east, and west radii with outstretched arms and counting all vertical stems less than 3 cm contacted by the arms or chest at 1.3 m above the ground. Basal area of shrub and tree stems was calculated using the actual DBH measurements for stems at least 3 cm and an estimate of 1.5 cm DBH for each stem less than 3 cm.

Foliage heights were determined at 20 points located at 1.6 m intervals along the north, south, east, and west radii of each circular plot. A 3-m tall pole (2.0 cm diameter) marked at 0.5 m intervals was placed vertically at each sampling point. We recorded the presence or absence of coffee foliage touching the pole within each height class. For height intervals above 3 m, we sighted along the pole and recorded the presence/absence of foliage in each of the following height intervals: 3–4 and 4–6 m. We used the upper limit of each height category to calculate the median maximum coffee height based on the two highest categories in each plot.

Plantations were visited during three periods (24 October–16 November 1994, 9 January–1 February 1995, 13 March–5 April 1995). Foraging observations were made most often between sunrise and noon, but some observations were made in the late afternoon. Observations were made by walking slowly though a plantation until a foraging bird was located. A foraging event was recorded five seconds after an individual was detected to avoid a bias toward the more conspicuous feeding techniques such as aerial maneuvers. To characterize foraging maneuvers, only a single foraging event was recorded from an individual during a morning to avoid the problem of auto correlation inherent in sequence data (Wagner 1981). The height of the location of the first maneuver was measured with an optical range finder. We tried to observe as many different individuals as possible, but for the rarer species we estimate that a maximum of 20% of the total observations were derived from the same individual. For the very abundant Bananaquit (*Coereba flaveola*), it was necessary to limit a morning's observation to a maximum of 3 individuals. Ovenbirds (*Seiurus aurocapilus*) were common ground foragers in the plantations (Wunderle and Latta 1996), but difficult to observe and therefore it was not possible to include ground foragers in this study.

Foraging maneuvers were classified into three major categories. We use the term "glean" to designate all "near-perch" maneuvers in which the forager remains on a perch and picks a food item from the substrate surface. This category includes all forms of reaching, hanging, and lunging. The term "probe" is used to designate all "near-perch" maneuvers in which a forager remains on a perch and obtains a food item from the under surface by probing, gaping, or pecking. Finally, we use the term "hover" to include all aerial

maneuvers in which the forager obtains a food item by leaving the substrate by leaping, or flying. While hovering, a forager can obtain food from a surface or the air by gleaning or from the under surface by probing.

The times between successive foraging maneuvers in the shade overstory and coffee understory were obtained by continuously dictating foraging observations into a cassette tape recorder. Each forager was followed for a maximum of 5 min or until it disappeared. Using a stop watch we calculated the average time between foraging maneuvers for each individual in which three or more successive foraging maneuvers were observed. The median time between each foraging maneuver was based on the means for each individual in the particular habitat (coffee or overstory).

Nonparametric statistical tests were used throughout the study because the data did not fit the assumptions of normality (Hollander and Wolfe 1973). Because of the absence of normality we used medians to describe central tendency and in the analyses, although we do provide means for descriptive purposes (foraging heights). Mann-Whitney U-tests were used to compare the median times between foraging maneuvers. A one-tailed Wilcoxon Rank Sum Test was used to test the null hypothesis that the median foraging height of a species was not above the median maximum coffee height. The variation in a species' median foraging height and its abundance in point counts or net captures (Wunderle and Latta 1996) was compared using a Spearman Rank Correlation. Multidimensional scaling (MDS) provided a quantitative method for defining foraging guilds useful for comparisons with other sites. Multidimensional scaling was used to visualize the foraging dissimilarities between 19 bird species in the plantations based on their proportional use of three different foraging substrates (*Inga vera,* coffee, other) and three food types (nectar, fruit/seed, animal). Dissimilarities were computed indirectly by use of Euclidean distances, which were standardized before MDS based on the Kruskal method with monotonic regression (SYSTAT 1992). All analyses were conducted using SYSTAT (ver. 5.3) on a Macintosh computer.

RESULTS

As expected, coffee had the greatest stem density in our plantations, although its contribution to the total basal area was relatively small because most stems were less than 3 cm DBH (Table 1). The predominant variety of coffee (*Coffea arabica)* in the shade plantations was the traditional "típica" variety, although "catorra" predominated in some of the larger plantations and was used to replace "típica" in some of the smaller plantations. The median maximum height of coffee in our plantations was 4.0 m, which defined the limit of the plantation understory. Bananas and plantains (*Musa* spp.) were also found in the understory, but constituted only a small proportion of the total basal area. Subcanopy trees included *Citrus* spp. and guava (*Psidium guajava*). *Inga vera* (Mimosoideae) predominated in the overstory and accounted for over half the total basal area of the plantations. The maximum canopy height averaged 15.6 ± 3.8 (SD) m and ranged from 9.2–22.0 m among the 27 plots. Other canopy trees such as roseapple (*Syzygium jambos*), royal palm (*Roystonia* sp.), American muskwood (*Guarea guidonia*) and Caribbean pine (*Pinus caribaea*) were rare in the plantations, but were more common along the edges of some plantations.

TABLE 1. Species composition, basal area, and importance value of plants in shade coffee plantations near Manabao and Jarabacoa, Dominican Republic.

Species	Density of stems, <3 cm DBH (stems/ha)	Density of stems, ≥3 cm DBH (stems/ha)	Basal area of stems ≥3 cm (m^2/ha)	Importance value of stems ≥3 cm
Coffea arabica	6907	744	2.26	14.74
Inga vera	50	206	10.73	69.99
Musa spp.	0	133	1.45	9.50
Citrus spp.	58	52	0.15	0.98
Persea americana	0	9	0.37	2.40
Syzygium jambos	0	6	0.31	2.02
Roystonea sp.	0	2	0.04	0.26
Psidium guajava	0	2	0.01	0.07
Guarea guidonia	0	2	0.01	0.07

We observed a total of 24 species foraging in the plantations, but restricted our analysis to 19 species for which we had adequate sample sizes. Of the 19 species, 13 were permanent residents, five were winter residents (Nearctic migrants), and one was a spring–summer resident (Neotropical migrant).

Foraging rates.—Adequate foraging rate samples were obtained for only two species of Nearctic migrants. Median time between foraging maneuvers in Black-throated Blue Warblers (*Dendroica caerulescens)* did not differ significantly (Mann-Whitney U = 177, $P > 0.05$) between coffee (median = 6 sec., n = 15) and *Inga* (median = 6 sec., n = 27). However, the American Redstart (*Setophaga ruticilla)* had significantly (Mann-Whitney U = 253.5, $P < 0.001$) shorter intervals in *Inga* (median = 7 sec., n = 25) than in coffee (median = 11 sec., n = 12).

Foraging heights.—The shade overstory

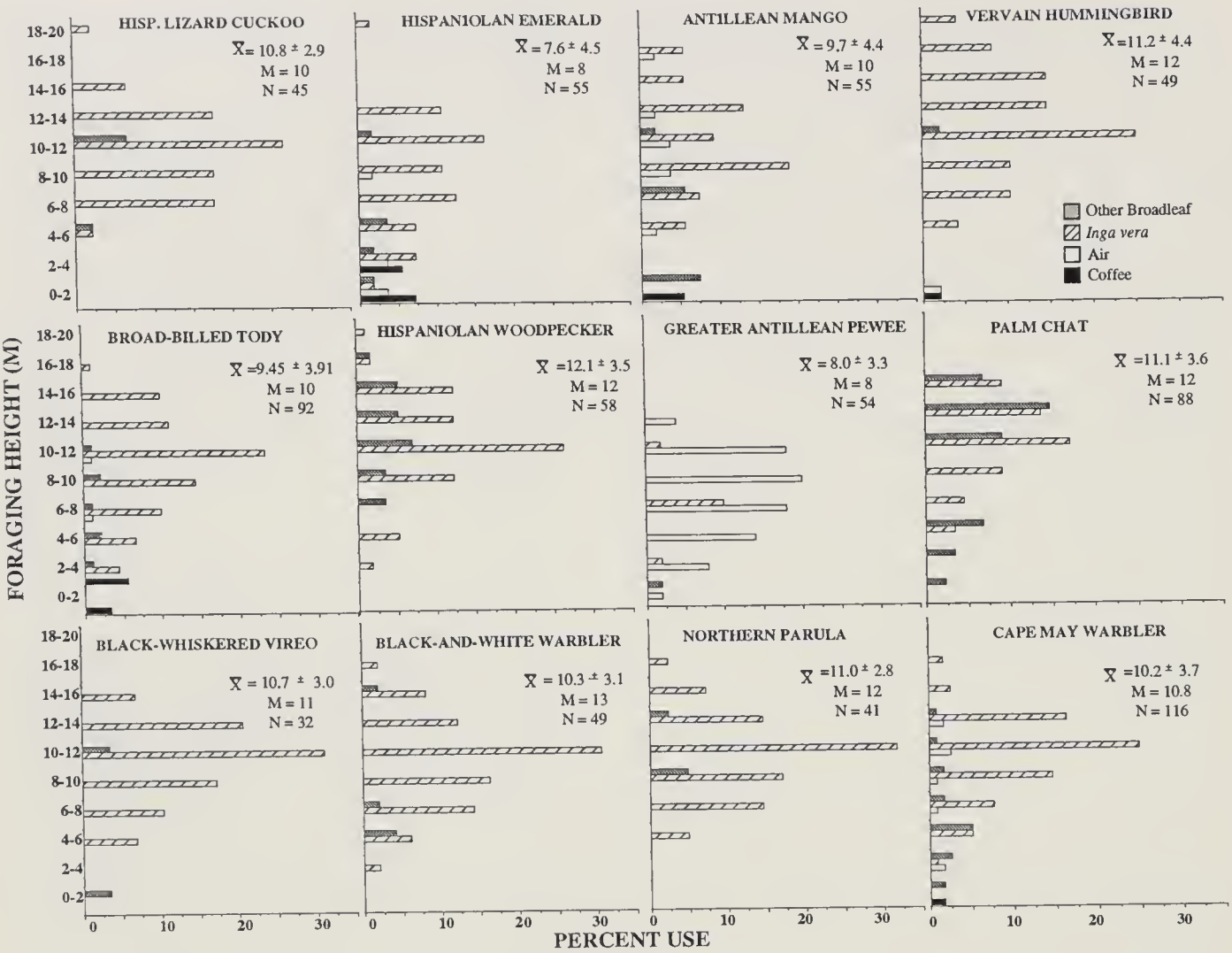

FIG. 1. Foraging height and location of first foraging maneuver after at least five seconds of observation for species in shade coffee plantations in the Dominican Republic. Foraging locations are given in legend. $\bar{X}$ refers to mean ± SD, M to median, and N to number of observations.

was the most important foraging site for almost all species, with 18 of the 19 species having median foraging heights significantly above the median maximum coffee height of 4.0 m (one-tailed Wilcoxon tests, all $P < 0.01$). All species were observed foraging in the *Inga* overstory, although they differed in how they divided their time between *Inga* and the coffee understory (Fig. 1). Eight species (42% of 19 species) foraged exclusively in the canopy or subcanopy and were not observed in the coffee understory. These canopy dwellers included Hispaniolan Woodpecker (*Melanerpes striatus*), Hispaniolan Lizard Cuckoo (*Saurothera longirostris*), Palm Chat (*Dulus dominicus*), Black-cowled Oriole (*Icterus dominicensis*), Black-whiskered Vireo (*Vireo altiloquus*), Black-and-white Warbler (*Mniotilta varia*), Northern Parula (*Parula americana*), and Black-crowned Palm Tanager (*Phaenicophilus palmarum*). Only the Narrow-billed Tody (*Todus angustirostris*) foraged mostly in the coffee understory (67% of observations) as shown by its median foraging height which was below the median maximum coffee height (one-tailed Wilcoxon test: $Z = -3.61$, $P < 0.001$). Although it did not feed in the coffee, the Greater Antillean Pewee (*Contopus caribea*) sometimes perched on the coffee and fed in the airspace between the coffee and the *Inga* canopy.

Foraging height and presence in sun coffee.—We expected that species which foraged primarily in the shade overstory above the coffee would be less abundant in sun coffee plantations than species which foraged in the coffee below the shade overstory. We tested this expectation by comparing the median foraging heights of the 19 foragers with their abundance in point counts and mist net cap-

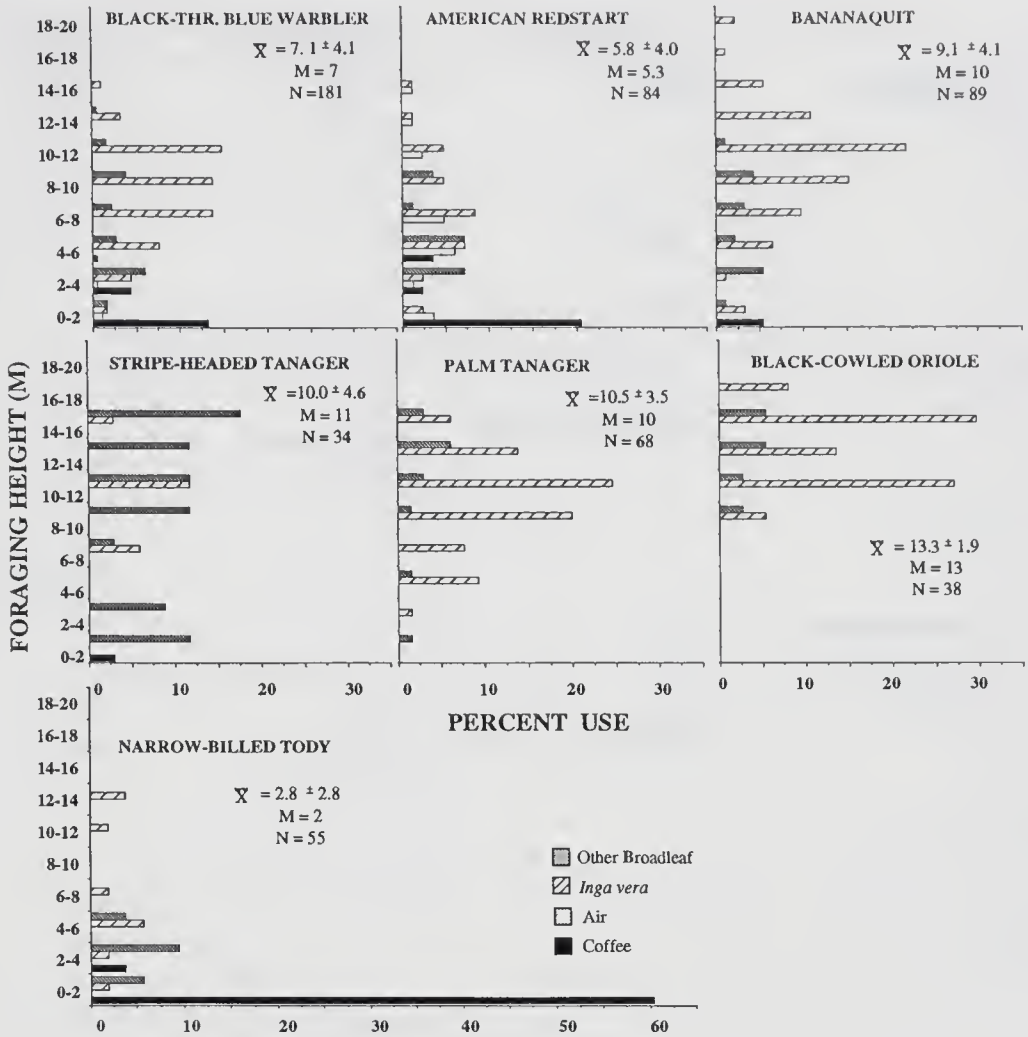

FIG. 1. Continued.

tures previously obtained in nearby sun coffee plantations (Wunderle and Latta 1996). As predicted, we found significant negative correlations between median avian foraging height in our shade plantations and abundance in sun coffee point counts (Spearman r = −0.62, df = 17, P = 0.005) and mist net samples (Spearman r = −0.58, df = 17, P = 0.009). Therefore, the higher a species forages in shade coffee plantations the less abundant it is likely to be in sun coffee plantations.

Foraging substrate.—Within *Inga* trees, the leaves were the most commonly used foraging substrate, on which 95% of all species (n = 19) foraged at least some of the time for invertebrate prey (Fig. 2). *Inga* leaves were the major foraging substrate (> 50% of observations) for Black-whiskered Vireo, Northern Parula, Broad-billed Tody (*Todus subulatus*), and Hispaniolan Lizard Cuckoo. *Inga* flowers were the next most important foraging substrate visited by 63% of the species. *Inga* flower visits accounted for over half the foraging observations for Vervain Hummingbird (*Mellisuga minima*), Black-cowled Oriole, Bananaquit, and Hispaniolan Emerald (*Chlorostilbon swainsonii*). The next most commonly used substrate was the *Inga* wood (trunk, branch, twig), upon which 58% of the birds foraged. *Inga* wood accounted for over half the observations of Hispaniolan Woodpecker (branches and trunk) and Black-and-white Warbler (branches and twigs). Less than half (47%) the species were observed feeding on or from *Inga* epiphytes. Epiphytes were gleaned or probed by 42% of all species but only 16% of all species consumed epiphyte fruits. Epiphyte foraging constituted only a small portion of a species' foraging visits, as evident in the two species which foraged most commonly on epiphytes: Stripe-headed Tanager (*Spindalis zena*; 36% of all observations, all fruit) and Black-crowned Palm Tanager (16% of all observations; 4 invertebrate, 6 fruit). *Inga* fruits were not present during most of the study. Perhaps as a result, they were the

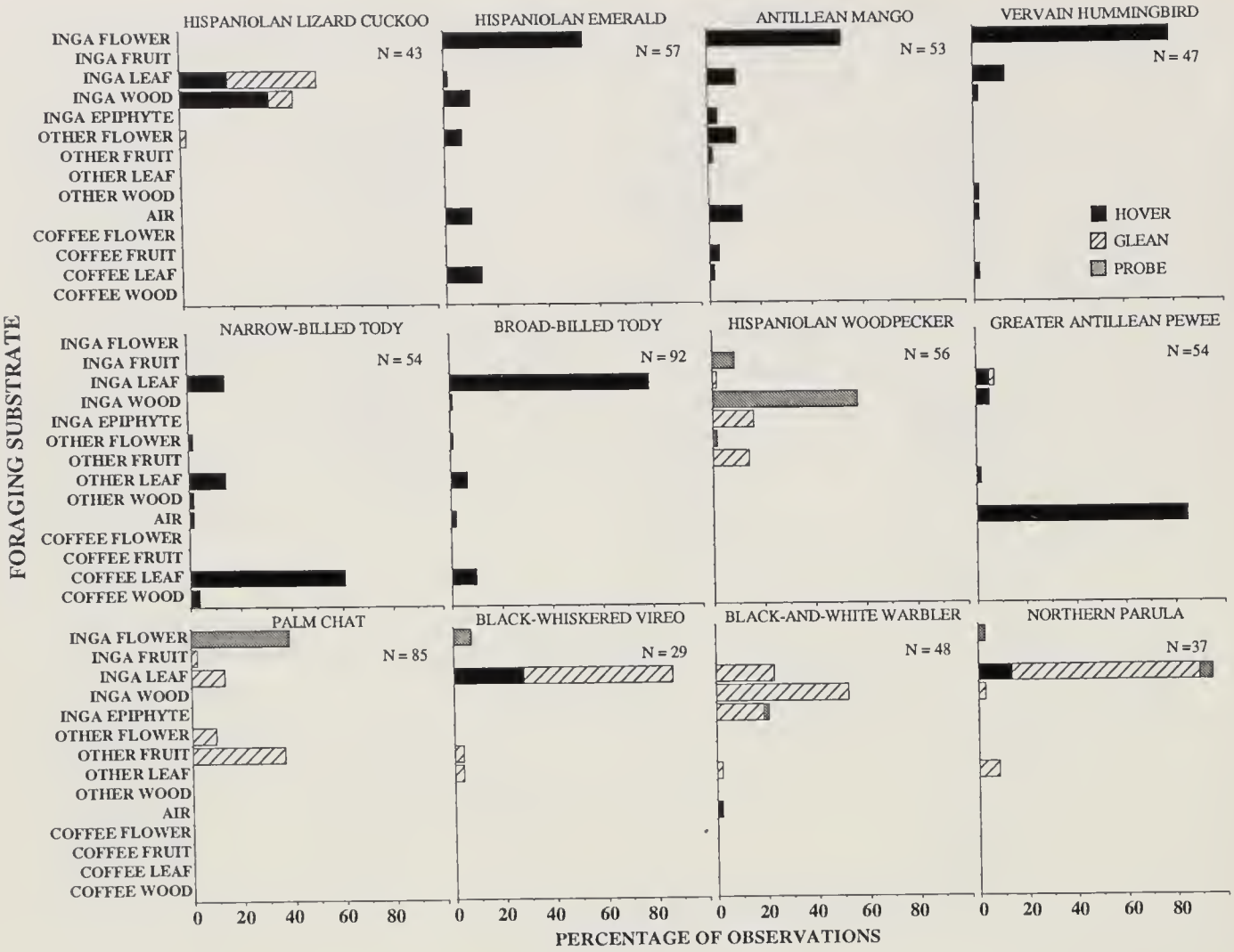

FIG. 2. Foraging substrates and three foraging maneuvers used by birds in shade coffee plantations in the Dominican Republic. Each observation (N) based on first substrate and maneuver used after at least five seconds of observation in a morning.

least commonly used substrate on the tree, used by only 26% of the species (mostly for invertebrate prey?), and at most, constituting only 9% of a species' foraging substrate (i.e., Hispaniolan Woodpecker).

Within coffee, the leaves were also the most commonly utilized substrate as evident in coffee leaf use by 42% of the 19 species. Coffee leaves were especially important for Narrow-billed Tody (62% of observations), but constituted less than a quarter of the foraging observations in the others (American Redstart, 24%; Black-throated Blue Warbler, 14%; Hispaniolan Emerald, 4%). The remaining parts of the coffee were used by only a relatively small percentage of the species (coffee wood, 21%; coffee fruit, 21%; coffee flower, 5%).

In addition to substrates in *Inga* and coffee, birds also foraged on substrates of the less abundant plant species. For example, flowers of other species (excluding coffee or *Inga*) were visited by 52% of the species, but at most constituted only about 10% of a species' diet (e.g., Antillean Mango, 11%; Bananaquit, 10%). *Syzygium* flowers were the most commonly used of the less abundant plant species (visited by 39% of the species). Fruits other than those of coffee and *Inga* were also consumed by 52% of the species, but constituted an appreciable portion of the diet in only two species (Palm Chat, 39%; Stripe-headed Tanager, 33%). The most important fruits appeared to be those of *Roystonea* (consumed by 28% of the species) and *Miconia* (consumed by 22% of species). In addition to leaves of coffee and *Inga*, 52% of the bird species fed from the leaves of a variety of other less abundant plants (8 plant species). At most these constituted only 12% of a species' foraging time (American Redstart). The most important leaves were those of *Citrus* spp. which were used by 21% of the species.

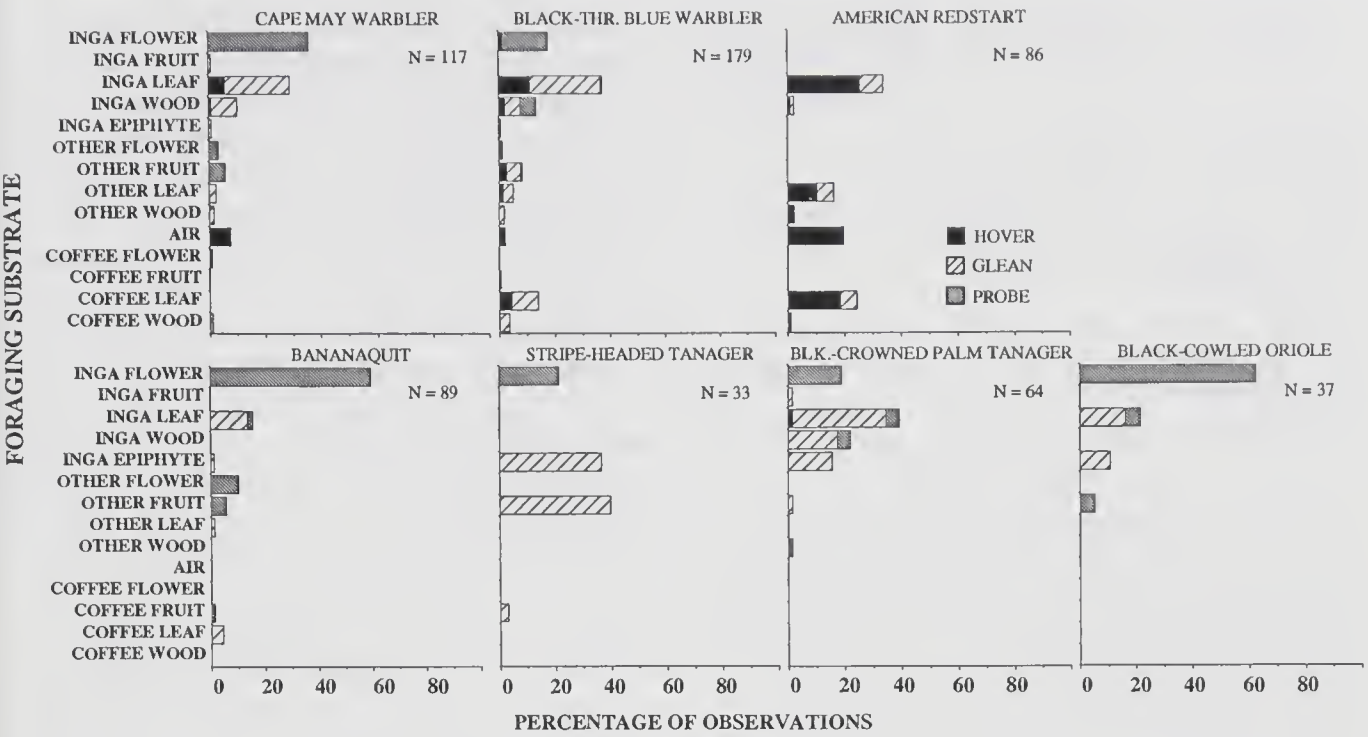

FIG. 2. Continued.

Foraging on woods other than coffee and *Inga* was uncommon and occurred in only 32% of the species and never constituted more than 2% of a species' foraging time.

Foraging maneuvers.—Individual species were usually consistent in their foraging maneuvers when feeding on similar substrates in coffee and *Inga* (Fig. 2). The only exception was the leaf probe maneuver used to obtain invertebrate prey from rolled or bound *Inga* leaves by Northern Parula, Black-throated Blue Warbler, Bananaquit, Black-crowned Palm Tanager, and Black-cowled Oriole. Leaf probing was absent in birds foraging in coffee, because there were no rolled or bound coffee leaves.

Species differed in their use of various foraging maneuvers while feeding in the plantations. For example, hovering was found in 68% of the species, but it was the predominant maneuver in only 42% of the species. Some species used hovering exclusively, such as hummingbirds which probed flowers or picked invertebrates from the air or leaf surfaces. Hovering also was the only maneuver used by both species of todies as they gleaned invertebrates from the undersides of leaves, and was the predominant maneuver used by Greater Antillean Pewees to capture insects in the air. Hovering was the predominant maneuver used by American Redstarts to capture invertebrates on leaf surfaces and in the air, although gleaning was also used. The leaps predominantly used by Hispaniolan Lizard Cuckoos to capture both lizards and invertebrate prey were classified as hovers, although cuckoos also gleaned prey from wood and leaf surfaces.

Gleaning was used by 68% of the species, although it was the predominant maneuver in only 32% of the species. Black-and-white Warblers gleaned mostly from wood surfaces or epiphytes on wood surfaces (lichens). Both Black-whiskered Vireo and Northern Parula commonly gleaned *Inga* leaves and, less frequently, hovered to take invertebrates from leaf surfaces. Gleaning prey from a variety of substrates with some probing characterized Black-crowned Palm Tanagers. Gleaning was the predominant maneuver used by Palm Chats, mostly to remove fruit, but they sometimes probed *Inga* flowers. Although gleaning was the predominant maneuver used by Black-throated Blue Warblers, they also hovered and probed a variety of substrates and were one of the most versatile foragers in the plantations (with Cape May Warbler, *Dendroica tigrinum*, see below).

Probing while perched on the substrate occurred in 53% of the species, but it was the predominant maneuver in only 26%. If the flower probes of hovering hummingbirds are

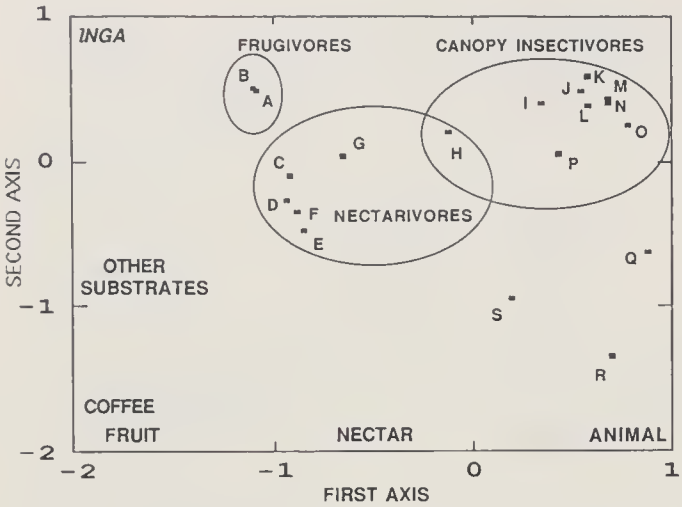

FIG. 3. Multidimensional scaling on two axis of foraging birds in shade coffee plantations in the Dominican Republic, based on three foraging substrates (coffee, other substrates, *Inga vera*), and three food types (fruit/seed, nectar, animal). Letters refer to the following species: A. Stripe-headed Tanager, B. Palm Chat, C. Bananaquit, D. Vervain Hummingbird, E. Hispaniolan Emerald, F. Antillean Mango, G. Black-cowled Oriole, H. Cape May Warbler, I. Black-crowned Palm Tanager, J. Black-whiskered Vireo, K. Hispaniolan Woodpecker, L. Northern Parula, M. Hispaniolan Lizard Cuckoo, N. Black-and-white Warbler, O. Broad-billed Tody, P. Black-throated Blue Warbler, Q. American Redstart, R. Narrow-billed Tody, S. Greater Antillean Pewee.

included, then probing occurred in 68% of the species, with 42% using it as the predominant maneuver. Probing was the predominant maneuver for Black-cowled Orioles, Bananaquits, and Cape May Warblers, primarily for nectar in flowers, but sometimes used for obtaining fruit juices. Hispaniolan Woodpeckers mostly probed wood, but also *Inga* fruit and flowers of *Syzygium*.

Foraging ordination.—Multidimensional scaling (MDS) enabled us to visualize dissimilarity among the 19 bird species based on their proportional use of foraging site and food type (Fig. 3). The first MDS axis separated species primarily on the basis of diet, with those species taking a high proportion of animal prey at one extreme on the axis in contrast to those with a high proportion of plant material on the other (nectarivory and frugivory). The second axis separated foragers on the basis of foraging site, with species foraging mostly in coffee at one extreme of the axis, in "other" plant category in the center, and in *Inga* at the other extreme. The third axis only weakly separated species foraging primarily in the "other" plant category from those foraging in *Inga* and coffee. Tight clusters were apparent for nectarivores, which fed mostly in the canopy (Antillean Mango, Hispaniolan Emerald, Vervain Hummingbird, Bananaquit, Black-cowled Oriole) and canopy insectivores (Black-crowned Palm Tanager, Hispaniolan Woodpecker, Hispaniolan Cuckoo, Broad-billed Tody, Black-whiskered Vireo, Black-throated Blue Warbler, Northern Parula, Black-and-white Warbler). Palm Chats and Stripe-headed Tanagers clustered together on the first two axes because of their tendency to feed on nectar from *Inga* flowers and consume fruit from other plants.

DISCUSSION

Given the preponderance of foraging observations in the *Inga* overstory, it is apparent that the characteristics of *Inga vera* strongly influence the foraging behavior and presence of birds in these plantations. Our finding that all species fed from *Inga* leaf surfaces at least some of the time, suggests that the *Inga* leaves in our plantations hosted an abundant invertebrate fauna. Indeed, *Inga* leaves are known to host a variety of invertebrates including folivores such as grasshoppers, katydids, lepidopteran larvae, and beetles and others that bind together leaves including spiders, small orthopterans, skipper larvae, and microlepidoptera (Koptur 1983). Although the extrafloral nectaries on *Inga* leaves may attract various ants, parasitic wasps, and flies that deter herbivores (Bentley 1977, Koptur 1983), no invertebrates were detected during our inspections of the nectaries on both young and old leaves. Caterpillars and leaf damage were often evident in the canopy and at times the frass rain was audible in some plantations. Not surprisingly, several bird species were observed feeding on caterpillars in the *Inga* canopy.

Flowers of *Inga vera* have nocturnal anthesis and are visited at night by bats and hawkmoths (Salas 1967, 1974), but evidently nectar remains in the morning when most bird visits were observed. *Inga vera* flowers have been found to be attractive to a variety of avian nectarivores during restricted flowering periods, at least in areas of seasonal rainfall (Wolf 1970, Greenberg et al. 1997b). In our plantations, some *Inga* flowers were present

throughout the duration of our study, but flowers were most abundant in March–April (pers. obs.). Despite this seasonal variation in *Inga* flower abundance, the most abundant nectarivores visited flowers in the same proportions (relative to insectivory) throughout the study period, although the numbers of nectarivores increased with an increase in flowering (pers. obs.). The March–April flowering peak in this study was later than in the previous two seasons when flowering peaked in January. As a result of the later flowering, *Inga* fruiting was also delayed and most fruits had not ripened by the end of our study. Therefore it is likely that *Inga* fruit consumption was under-represented in this study relative to previous years when we occasionally encountered parrots and parakeets feeding on *Inga* pods during the same time period.

Epiphytes and plant parasites growing on the *Inga* were not abundant in our plantations, which undoubtedly explains their relatively low levels of use by most birds. Lichens were the most abundant epiphytes and were probed or gleaned for invertebrates by several species including Black-and-white Warbler, Hispaniolan Emerald, Black-throated Blue Warbler, and Hispaniolan Lizard Cuckoo. Bromeliads were probed for invertebrates by Black-crowned Palm Tanagers, Hispaniolan Woodpeckers, Bananaquits and Greater Antillean Grackles (*Quiscalus niger*). Mistletoe fruits were consumed most frequently by Stripe-headed Tanagers, but were also taken by Black-crowned Palm Tanagers and Black-cowled Orioles. Also, Antillean Euphonias (*Euphonia musica*) probably would have been more abundant in our plantations had mistletoe been more common given the reliance of euphonias on mistletoe fruit (Snow 1981).

Almost all of the foraging maneuvers in coffee were associated with insectivory (includes insects and spiders). This preponderance of insectivory is consistent with mist net results from the same plantations (Wunderle and Latta 1996). These results, based on diet classification from the literature, indicate that 50% of the 358 birds captured in the coffee were primarily insectivorous compared with 43% nectarivores and 6.7% fruit/seed eaters. Given our foraging observations, it is likely that most of the captured nectarivores were actually feeding on invertebrates in the coffee when captured. Thus, it appears that foraging birds use coffee plants primarily to obtain invertebrate prey.

Despite the preponderance of foraging for invertebrates in the coffee, most birds foraged infrequently in coffee, and for American Redstarts the foraging rates were lower in coffee than in the *Inga* overstory. These findings undoubtedly are due to relatively low invertebrate densities on the coffee plants as noted by Greenberg and coworkers (1997a) who found arthropod biomass per 100 g leaf biomass to be approximately 6 times greater for *Inga* than shade coffee. Evidence for low densities is also supported by our observations that insect damage to coffee leaves was rare in contrast to the obvious damage in the *Inga* canopy (pers. obs.). Indeed, others have noted that insect damage to coffee leaves is unusual (Le-Pelly 1973), in part because young coffee leaves have an abundance of protective alkaloids and the older leaves are very tough (Frischknecht et al. 1986). Also, it is likely that the transfer of coffee to the Neotropics left behind many of the Old World herbivores that evolved mechanisms to overcome its defenses, as often occurs with the transfer of cultivated plants (Perfecto et al. 1996). Our own surveys of invertebrate abundance on coffee leaves in these plantations (Wunderle and Latta 1996) indicate levels of abundance three times lower than are found in native, moist broadleaf forest elsewhere in the Caribbean (Askins and Ewert 1994).

Given the importance of the overstory to avian foragers in our plantations, it is not surprising that canopy dwellers were less abundant in the absence of a canopy in nearby sun coffee plantations (Wunderle and Latta 1996). For instance, of the 9 species that foraged exclusively in the *Inga* overstory, seven (Black-cowled Oriole, Black-whiskered Vireo, Greater Antillean Pewee, Hispaniolan Lizard Cuckoo, Palm Chat, Northern Parula, Black-and-white Warbler) were absent from point counts in sun coffee; Hispaniolan Woodpeckers were present in the sun coffee, but significantly less frequently; and Black-crowned Palm Tanagers were less frequent in sun coffee, but not significantly. Our observations indicate that nectarivores (Vervain Hummingbird, Hispaniolan Emerald, Antillean Mango, Bananaquit, Cape May Warbler) mostly fed on *Inga* flowers in

the shade plantations, and as expected in the absence of flowering, each showed significantly lower abundance in sun coffee. Insectivores that fed mostly in the *Inga*, but descended into the coffee were also found in the sun coffee at counts equivalent to (American Redstart, Broad-billed Tody), or significantly higher (Black-throated Blue Warbler) than counts in shade plantations. Finally, the insectivorous Narrow-billed Tody foraged mostly in coffee and was also significantly more abundant in sun than shade plantations. Thus, species most dependent on the shade overstory for foraging are most likely to decrease in the absence of a shade overstory in sun plantations, while those that can forage in the coffee may be present, if not abundant, in some sun plantations (assuming low or no pesticide use).

Other cultivated crops in our plantations provided foraging opportunities, but they did not appear to be utilized disproportionately in relation to the plants' abundance. For example, bananas and plantains, despite their relative abundance in the plantations were infrequently used by foraging birds. The leaves were only rarely gleaned for invertebrates and the flowers sometimes visited for nectar (Antillean Mango, Bananaquit, Cape May Warbler). Other plants such as citrus, avocado, and guava appeared to be utilized by foragers in direct proportion to their abundance in the plantation. Although these crops may not have attracted additional bird species to the plantations, they may contribute to a plantation's attractiveness to birds by providing resources out of synchrony with the *Inga* overstory. In addition such sub-canopy trees as citrus and avocado provide additional foliage layers below the *Inga* canopy that serve as additional foraging substrate for insectivores.

Some of the non-agricultural plants in the plantations appeared to be important in attracting birds to the plantations. For example, royal palms attracted Palm Chats and Black-cowled Orioles. Both species were present only where palms occurred in the immediate vicinity, presumably because of nesting requirements, although Palm Chats frequently fed on palm fruit. Royal palm fruits are consumed by a diversity of species (Wunderle, unpubl. data), and the rarity of palms limited our fruit consumption observations to only 5 species. Fruits of the Melastomataceae are also known to be important for a variety of bird species (Snow 1981), but their rarity too may have limited our observations to only 4 species, all of which fed elsewhere in the plantations. *Syzygium* flowered throughout the duration of the study and was visited by 7 species, all of which were common at *Inga* flowers.

The results of our study suggest that a coffee plantation's attractiveness to birds is enhanced with the abundance, variety, and consistency of food resources in a plantation. This finding applies mostly to the shade overstory or plantation border, as the coffee plants alone provide limited food resources or foraging substrates for most species in this study. A diversity of plant species in the overstory or border attracts more birds, particularly if the plants are asynchronous in flowering and fruiting and extend the time period over which resources are available in a plantation. Given these traits, shade coffee plantations can provide food resources for a variety of bird species in agricultural areas, and thereby help maintain avian abundance and diversity in agricultural regions. Furthermore, these findings suggest that shade coffee plantations could serve as an effective buffer between forest reserves and surrounding agricultural landscapes.

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Short Communications

Wilson Bull., 110(2), 1998, pp. 282–285

Discovery of a Harlequin Duck Nest in Eastern North America

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ABSTRACT.—Harlequin Ducks (*Histrionicus histrionicus*) were observed breeding on a tributary of the northwestern arm of Hebron Fiord, Labrador. Peak population numbers were 11 males and 13 females on 17 June; females consistently outnumbered males. Breeding was confirmed by the presence of a nest with eggs and the presence of downy chicks. *Received 10 Feb. 1997, accepted 22 Jan. 1998.*

Harlequin Ducks (*Histrionicus histrionicus*) have a disjunct, Holarctic distribution with distinct populations in northwestern North America and Asia, Iceland, Greenland, and eastern North America (Palmer 1976, Montevecchi et al. 1995). They are unique among northern hemispheric waterfowl in nesting primarily on swift-flowing streams located in undisturbed forested, montane, and tundra habitats at coastal and inland locations (Bengtson 1972, Dzinbal 1982, Cassirer and Groves 1991). In Iceland, most nests were within 5 m of the water on islands and riverbanks. Nesting occurred on the ground under dense willow (*Salix* spp.) shrub, and less frequently in rocky cavities and short vegetation and grasses (Bengtson 1972). The few known nest sites in North America have been on the ground, on woody debris, on cliff ledges, and in rock and tree cavities near stream banks or, in one case, on a small maritime island (Merriam 1883, Campbell et al. 1990, Cassirer et al. 1993).

In eastern North America, Harlequin Ducks may have declined to less than 1000 individuals (Vickery 1988, Goudie 1989) and have been listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Goudie 1991). We report here on the discovery of the first confirmed nest in Labrador (see Todd 1963). Nests have also been found for the first time in Québec (Robert 1996; S. Brodeur, pers. comm.). We also present information on brood amalgamation and breeding phenology, which, in addition to the nest-site description, will aid future research.

STUDY SITE AND METHODS

We conducted this study from 8 June to 14 August 1996 on "Harlequin Brook" (58° 09′ 40″ N, 63° 04′ 45″ W), a tributary of the Ikarut River in the northwestern arm of Hebron Fiord, Labrador. The brook extends 12 km from the estuary to a lake outlet at 200 m elevation. Canyons at 4–6 and 9.5–11 km above the estuary separate it into three distinct sections. Coastal tundra habitat in Hebron Fiord of rolling moorland rising to 400–700 m elevation with dense, shrub-covered sections along streams is similar to montane habitat in Iceland (Bengtson 1972).

The fiord was ice-bound and ice and snow covered river banks and islands in early June. By mid-June, much ice and snow was breaking off river banks and islands, but high spring water levels flooded much of the islands through the third week in June. Ice was retreating from the heads of the fiord by mid-June and the fiord was clear of ice on 27 June.

We kept regular records of Harlequin Ducks in the lower 2 km of the brook and explored the upper reaches every 2–3 weeks. Data presented here summarize maximum numbers of males and females counted per day. A total of 48 person-h were spent searching for nests. We focused our search efforts within 5 m of the stream on shrub covered banks and islands.

RESULTS

Maximum numbers of Harlequin Ducks counted on the entire brook were 11 males and 13 females on 17 June. Females generally outnumbered males throughout the period males were present. Pairs were more dispersed along upper than lower portions of the brook during the pre-laying period. Common sightings in the lower 2 km of the brook were of

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small groups on or in the vicinity of a well-used roosting site on a small gravel bar in smooth water 1.7 km from the estuary (e.g., 7M, 7F on 8 June; 8M, 10F on 11 June; 6M, 10F on 17 June; 5M, 7F on 30 June). A maximum of 3 males and 4 females (in groups of 2 pair, 1 pair, and 1 female), and 1 pair were counted above the first and second canyons, respectively, on 21 June. Similar numbers of males were present throughout June, after which one was seen on 4 July, and the last was seen on 12 July. Throughout July, 3–7 females that we concluded were failed breeders or non-breeders frequented roost sites and feeding areas at all times of day.

A down-lined, 28 cm diameter nest containing 6 eggs was discovered on 21 July on a 12 × 45 m island densely covered with overhanging willow and alder (*Alnus crispa*) shrubs. The incubating female did not flush from the nest until we approached to within 2 m. The nest was situated among some small stones and a mound of dry leaf litter at the base of a clumped-stem, 2.3 m high alder. It was 0.5 m above water level in the middle of the tapered, upstream, northern end of the island, 4.4, 5.1, and 4.6 m from the north, east and west edges, respectively. Shrub canopy within a 5 m radius around the nest was 85% complete and 2.2 m high, and included 5 willow and 19 alder shrubs with an average of 16 (range 7–33) and 13 (range 2–32) stems per shrub, respectively. There was little understory vegetation adjacent to the nest, and ground cover within a 5 m radius was 10% moss, 30% herbaceous vegetation, and 60% bare ground and leaf litter. Shrubs overhung the brook by 0–0.6 m. Channels east (to the edge of the brook) and west (to an adjacent island) of the island were 20 and 4.1 m wide, 0.5–1.0 and less than 0.5 m deep, with some riffles, and flow rates of 1.25 and 1.11 m/s over boulder substrates, respectively. The island was one of about 20 similarly vegetated islands in a braided section of the brook with an overall width of 80 m (including islands) located 2.5 km from the estuary. All islands and adjacent stream banks in this area were searched for nests.

Eggs had been hatched for a few days when we revisited the nest on 2 August. Down and feathers from the edge of the nest had been carefully folded into the center completely covering the six hatched eggshells.

First broods of five and six ducklings were seen on 29 July on a nearby stream (58° 11′ 30″ N, 62° 47′ 20″ W), and broods of eight and six, three, and one ducklings were first seen on Harlequin Brook on 2, 3, and 4 August, respectively. All ducklings were small and downy (1a-1b) when first observed and estimated ages for those broods (Gollop and Marshall 1954) indicated hatching dates in the last week of July. All broods were diligently guarded by single females, except the single duckling which was observed feeding as far as 100 m upstream from a "neglecting" female. The broods of six and one ducklings were found 4 km upstream from the other broods beyond an intervening stretch of canyon with many waterfalls and rapids. The lone duckling was not seen again but the female and brood of six were observed gradually working their way upstream between 2 and 5 August, after which we conducted no further observations. The broods of eight and three ducklings were first observed in the same section of the brook where the nest had been found and we assumed that one of them had hatched from that nest. We saw those broods further downstream on 4 August, and the brood of three was seen at 1.2 km upstream from the estuary on 5 August. On 10 August, we found only one brood of 10 ducklings with a single female in this area, which was undoubtedly an amalgamation of the two broods. They were seen again on 11 and 13 August working their way up and down the lower 2 km of brook, always with only a single female.

DISCUSSION

Timing of hatching in the last week of July is 2–4 weeks later than dates reported for Idaho (Cassirer and Groves 1991), Montana (Kuchel 1977), and Alaska (Dzinbal 1982), and is similar to median dates in Iceland (Bengtson 1972) and Wyoming (Wallen 1987). Differences may be due to spring conditions and altitudinal and latitudinal effects on timing of snow melt (Bengtson 1972, Wallen 1987, Cassirer and Groves 1991). Laying (assuming a 28 d incubation period; Bengtson 1972) apparently peaked just after snow melt and recession of flood waters near the end of June on Harlequin Brook.

A maximum of 11 males and 13 females were observed in 1996. Our observations of

greater numbers of females than males is contrary to the dominance of males reported in other studies (Bengtson 1966, 1972; Kuchel 1977; Inglis et al. 1989). Reasons for this difference are unknown and possible sources of differential mortality should be considered. Assuming that the number of males corresponds to the number of breeding pairs yields a density estimate of 0.92 pairs/km, slightly less than the mean of 1.3 pairs/km reported for streams in Iceland (Bengtson 1972). Regular observations of 3–7 non-breeding females during July suggest that only half of the females present bred in 1996. Aerial surveys in Labrador also indicate high incidence of non-breeding females (Goudie et al. 1994; see also Bengtson and Ulfstrand 1971).

The nest site and clutch size were similar to those described in Iceland (Bengtson 1972). Although our single nest find supports the merit of searching through dense shrub habitat, other possible nest sites, such as rock cavities and cliff ledges, should not be ignored.

Behavior of adults and broods differed in the upper and lower brook. In the lower brook, adults tended to gather at a communal loafing site or "club" (Bengtson 1966) below the nesting area, especially before egg-laying (see also Kuchel 1977). Pairs were dispersed along the upper brook at that time. The canyon may have presented a barrier to brood movement because ducklings hatched above the canyon tended to move upstream, while broods below the canyon worked their way up and down the lower 2–3 km of brook and made some use of the estuary for feeding.

Brood amalgamation is common in waterfowl when broods hatch synchronously and brood-rearing habitats overlap (Afton and Paulis 1992), as was the case in the lower section of Harlequin Brook. Brood amalgamation following abandonment of older ducklings, and groups of 2–3 females sharing mixed-age younger broods with no indications of one female "robbing" ducklings from another have been reported in Iceland (Bengtson 1966, 1972). Only one female accompanied the amalgamated brood of 10 downy ducklings over the three days that we observed them. We did not observe her interacting with other females in the area. One female appeared to have abandoned her brood. We suspected partial amalgamation had occurred when we first observed the broods of three and eight ducklings because one brood probably came from the nest we located with six eggs; hatching success is normally high (Bengtson 1972).

Implications for survey times in northern Labrador indicate that pair counts are probably best carried out in mid-June before egg-laying and the departure of males at the end of June. Brood counts should be conducted in early August.

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Maturation and Variation of Head Characteristics in Sandhill Cranes

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ABSTRACT.—We evaluated eye color, bill color, and head plumage characteristics in 836 known-age Sandhill Cranes (*Grus canadensis*) captured in Florida between 1974 and 1995. Eighty-three birds were recaptured 1–16 years later. There were noticeable variations in eye color and head plumage among individuals and between birds 20 months or less of age and those 21 months and older. These variations may be representative of the relatively high genetic diversity in Sandhill Cranes and be criteria for mate selection.
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Birds that exhibit delayed onset of reproduction may go through a series of plumage changes before attaining their characteristic adult appearance. Sandhill Cranes (*Grus canadensis*) are sexually mature at two to three years, but gross plumage characteristics distinguish juveniles from adults only in their first year (Tacha et al. 1992). Adults are pale mouse gray to ashy slate gray with a gull gray to white cheek, an unfeathered crown of begonia rose, and a pallid to mouse gray nape (Ridgway and Friedmann 1941) that may be darker in some populations. The mikado brown natal plumage is gradually replaced with pale mouse gray plumage through fall and winter of the first year (Tacha and Vohs 1984, Tacha et al. 1992). Iris color at hatching is dark raw umber, changing during the first year to orange (Tacha et al. 1992). The flesh-colored bill of hatchlings changes to a dark drab gray, fading to olive gray in the mid-mandibular area in adults (Tacha et al. 1992).

After January of their first year, juveniles cannot be easily distinguished at a distance from older birds (Lewis 1979). In hand, how-

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ever, individuals can be separated into four year classes: juvenile (3–12 months), first year subadult (12–24 months), second year subadult (24–36 months), and adult (≥ 36 months) based on plumage and molt characteristics (Lewis 1979, Nesbitt 1987).

Adult-plumaged Sandhill Cranes captured in Florida for other studies (Williams and Phillips 1972, Nesbitt and Williams 1990, Nesbitt and Carpenter 1993) showed variations in iris, cheek, bill, and nape coloration. We began recording head characteristics as part of routine handling in 1974 to investigate the possibility that these variations might be useful for aging birds beyond the first year. The opportunity to recapture some of the cranes made it possible to follow the changes in these head characters as individuals aged.

STUDY AREA AND METHODS

Greater Sandhill Cranes (*G. C. tabida*) and nonmigratory Florida Sandhill Cranes (*G. c. pratensis*) were captured on or near Paynes Prairie, Alachua County, Florida using oral tranquilizers applied to whole kernel corn (Williams and Philips 1973, Nesbitt 1984, Bishop 1991). Hatch dates for most eastern Greater and Florida Sandhill Cranes are from early March to late May (Tacha et al. 1992); so, 1 April was assigned as an arbitrary hatch date for all birds. The cranes were segregated into seven age groups (3–6 months, 6–9 months, 9–12 months, 12–18 months, 18–24 months, 2–3 years, > 3 years) based on date of capture or wing molt.

Iris color was compared to a color guide (Smithe 1975–1981) and ranked as amber, buff, buff-yellow, orange-yellow, spectrum orange, chrome orange, or flame scarlet. Clarity of the white cheek patch was ranked as not present (all gray), poorly defined (more gray than white), fairly well-defined (more white than gray), or well-defined (all white). The occipital area of the nape was evaluated for the presence or absence of brown (persistent juvenile plumage) or white feathering. White feathers in the nape were ranked as not present, 1–12 feathers, 12 to 24, > 24, or a more or less complete line.

The birds were individually color marked (Nesbitt et al. 1992) and banded with standard USF&WS numbered leg bands. Cranes were held until they recovered from the tranquilizer and then returned to the area of capture. Subsequent to marking, sex and population of origin were determined based on behavior and resighting location, respectively (Nesbitt et al. 1992).

RESULTS

Between 1974 and 1995, 836 known-age cranes were evaluated. Forty-seven birds first captured as adults were recaptured 1–16 years later [($\bar{x}$ = 3.6 ± 2.8 (SD) years], and 36 birds that were initially captured as juveniles or first-year subadults were recaptured as adults.

The most frequently occurring iris colors among adult cranes were chrome orange, flame scarlet, or spectrum orange, in descending order of frequency (Table 1). Juvenile iris color progressively lightened from amber to buff-yellow then darkened to spectrum orange or chrome orange by the middle of their second year. Two-year-old cranes showed a greater frequency of orange yellow than adults, but, by the third year, iris colors occurred at rates similar to adults. Remnant juvenile brown feathering persisted in some birds beyond the second year, but 83% had no brown feathers after 18 months (Table 1). Forty-three percent of the adult cranes showed some white feathering in the nape, with 7% showing a distinct line of white feathers across the nape. White feathering began appearing as the brown juvenile plumage was replaced, and, by 18 months, the rate of occurrence was similar to that of adults (Table 1). Cheek clarity rankings in 2–3 year olds and adults were similar; most (88 and 85% respectively) were either more white than gray or all white (Table 1). Ranking of juvenile cheek clarity was predominantly (100–66%) not present or mostly gray. Cheek clarity in one- to two-year old cranes approximated that of adults, with 77% ranked as more white than gray or all white.

The mean age after which no further changes in iris color were seen was 19.0 (± 4.1 SD, range 12–24) months for birds banded as juvenile or first year subadults and recaptured as adults. Cheek clarity became stable at 16.7 (± 4.4 SD, range 9–24) months. Brown feathers were no longer present in the nape at a mean age of 19.6 (± 3.8 SD, range 10–24) months. White feathering in the nape became fixed after a mean age of 16.5 (± 4.6 SD, range 10–24) months. Too little variation in bill color was noticed for it to be a useful characteristic.

Cranes initially banded as adults and recaptured one year or more later showed little change in any characters evaluated. Iris color and cheek clarity ranked the same in 97.9% of the recaptures; white feathering in the nape was the same in all recaptured cranes. The only case of iris color change (interval six years) was from chrome orange to flame scar-

TABLE 1. Occurrence (%) of head characteristics in Sandhill Cranes from Florida, 1974–1995.

Months of age (n)	Iris color[a]							Cheek clarity[b]				Nape								
												% Brown					# White			
	AMB	BUF	BUF YEL	ORG YEL	SPE ORG	CHR ORG	FL SCAR	NP	PD	FWD	WD	NP	10	11–30	31–50	>50	NP	1–12	13–24	>24	Line
3–6 (30)	20	37	32	10	10	00	00	60	40	00	00	04	04	07	14	72	45	35	14	07	00
6–9 (84)	08	14	46	08	21	01	00	21	68	10	01	02	09	18	23	48	14	51	15	21	00
9–12 (104)	04	11	38	13	16	16	02	21	45	28	06	04	17	25	28	27	21	40	18	19	03
12–18 (99)	01	02	13	18	36	27	02	00	21	45	34	55	29	15	01	00	43	32	01	09	14
18–24 (127)	00	00	08	21	20	40	10	00	26	45	29	83	16	02	00	00	52	35	08	02	04
24–36 (92)	00	00	04	08	24	48	16	01	14	53	33	92	08	00	00	00	61	25	07	01	06
>36 (300)	00	00	01	04	16	53	26	00	15	44	41	100	00	00	00	00	57	25	06	01	07

[a] Iris colors are AMB, amber; BUF, buff; BUF YEL, buff-yellow; ORG YEL, orange-yellow; SPE ORG, spectrum orange; CHR ORG, chrome orange; FL SCAR, flame scarlet.
[b] Cheek clarity: NP, not present, all gray; PD, poorly defined, more gray than white; FWD, fairly well defined, more white than gray; WD, well defined, all white.

let. The only case of change in cheek clarity was in a bird ranked as more white than gray initially, then mostly gray when recaptured one year later. These two changes in ranking, out of 47 recaptured adults were both near enough to their initial rank to suggest that the change may have been due to ranking error rather than to any actual change in the characters as a consequence of aging.

There were no significant differences between iris color ($P > 0.05$, $\chi^2_3 = 0.604$), white feathering of the nape ($P > 0.05$, $\chi^2_3 = 1.523$), or cheek clarity ($P > 0.05$, $\chi^2_3 = 3.976$) between Greater ($n = 35$) and Florida Sandhill Cranes ($n = 44$). Variation in iris color was not influenced by gender [$P > 0.05$ $\chi^2_2 = 1.569$ ($n = 53$ ♂, 51 ♀)]. White feathering in the nape and cheek clarity were also not affected by gender ($P > 0.05$, $\chi^2_3 = 2.608$, and $\chi^2_2 = 1.189$, respectively).

DISCUSSION

The four head characters we evaluated became fixed at 16 to 20 months and did not change further as the birds aged. The variations found in iris color, nape, and cheek characters were not associated with population or gender. These variations may be a sign of comparatively high genetic diversity within the populations of Sandhill Crane we evaluated. Genetic diversity indices for Florida and Greater Sandhill Cranes are high (heterozygosity 0.125 and 0.067 respectively) when compared with other crane species or to other populations of Sandhill Cranes (Dessauer et al. 1992).

Tacha (1988) found that cheek clarity affected social status in juveniles. Juveniles still in family groups during winter and spring had gray cheeks, while juveniles that were alone had white flecks in the cheek patch. He also found a lower than expected occurrence of completely gray cheeks in paired or parent cranes suggesting that the absence of white in the cheek may be a disadvantage for pair formation in adults.

Cheek patch color may function as a signal of social status in juveniles or as a sign of fitness in older birds as Tacha suggested. But, if greater variability of cheek patch color and other head characters within populations reflect greater overall heterozygosity, then these characters could also be important criteria for

mate selection. A mate choice system that favors increased heterozygosity may increase resistance to disease (Jarvi et al. 1995). A mating system that tends to maximize genetic heterozygosity could also facilitate the ability of a species to adapt to a changing environment and have other advantages.

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First North American Record of a Melanistic Osprey

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ABSTRACT—The first melanistic Osprey (*Pandion haliaetus*) for North America (second for the world) is described and shown. It was seen and photographed in southern Florida on 4 March 1997. *Received 25 Aug. 1997, accepted 13 Jan. 1998.*

The Osprey, *Pandion haliaetus*, in spite of its world-wide distribution, shows little geographic or individual variation in its plumage (Poole 1989, del Hoyo et al 1994). None of the regional bird handbooks; e.g., for the Western Palearctic (Cramp and Simmons 1980), for Africa (Brown et al 1982), for North America (Palmer 1988), or for Australia (Marchant and Higgins 1993); mention any aberrant plumages for the Osprey. Recently, Millon (1994) briefly described a melanistic Osprey seen in France. Herein I describe the first melanistic individual of this species for North America. A dark Osprey had been observed regularly in the same area of mangrove islands over the past three years by Frank and Georgia Garrett on their daily boat tours out of Chokoloskee, Florida. They took me to see this unusual bird and I observed and photographed it for over three hours on the afternoon of 4 March 1997.

As seen in Fig. 1, the head, underparts, and underwing coverts of this Osprey are dark brown, with some buffy markings visible on the underparts. The head is uniformly dark; the black eye-line of Ospreys with normal plumage is not noticeable, even at close range. The pale undersides of the flight feathers differ from those of normal Ospreys (Wheeler and Clark 1995) in that they lack any dark barring. The eye and leg colors and tail color and pattern are the same as those of normal Ospreys, as are its vocalizations.

When I first saw this unusual bird, it was standing on a typical Osprey nest on a small mangrove island in the western end of Everglades National Park, approximately 5 km ssw of the town of Chokoloskee. The Garretts told me that they saw this bird build the nest. Another nest that it had built on an adjacent island was taken over by a pair of Ospreys in normal plumage three years previously.

Terres (1980) considers melanism to be an abnormal plumage, whereas Gross (1965) and Sage (1962) consider that there are both "normal" and "abnormal" melanism—normal being that of polychromatic species, with the dark birds comprising the dark morph, and abnormal being that of monochromatic species. Gross (1965) reported melanism, both normal and abnormal, in only 29 species of North American birds.

I never saw this dark bird in the company of another Osprey. I watched it hunt for more than 5 minutes on two forays—hovering for a while in one location and then moving to another, in typical Osprey fashion. On one foray, it caught a fish and took it to a perch and ate the fish entirely, not sharing with another Osprey. The Garretts have never, in more than three years of observations, seen this bird in regular close association with another Osprey, as would be expected if it were mated.

Plumage color has little effect on mate selection in polychromatic species, because most individuals of these species mate randomly regardless of color morph. The dark coloration of birds like this unusual Osprey may obscure plumage features necessary for mating, e.g., the dark carpal patches on white underwings of Ospreys in normal-plumage [see Olsen (1995) for a discussion of plumage social signals.]. It is also possible that species that are polychromatic are so because in the past aberrant individuals were able to mate with normal birds and thus pass on their dark genes, which are usually dominant when heterozygous (Sage 1962). Monomorphic species would remain so when the occasional melanistic individuals cannot mate and pass on their genes.

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FIG. 1. First melanistic Osprey recorded in North America.

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Red-cockaded Woodpecker Cavity Tree Resin Avoidance by Southern Flying Squirrels

Richard R. Schaefer[1,2] and Daniel Saenz[1]

ABSTRACT.—While examining Red-cockaded Woodpecker (*Picoides borealis*) cavity contents in eastern Texas, we observed cavity tree resin avoidance by southern flying squirrels (*Glaucomys volans*). The tree surface around an active Red-cockaded Woodpecker cavity is coated with sticky resin which flows from resin wells created by the woodpecker. The southern flying squirrel is a competitor for Red-cockaded Woodpecker cavities and is known to be quite capable of entering active cavities in trees with a well developed resin coating. However, our observation indicates that in some circumstances the resin coating can offer some deterrence. *Received 6 March 1997, accepted 18 Aug. 1997.*

The Red-cockaded Woodpecker (*Picoides borealis*) excavates roosting and nesting cavities in live southern pines (*Pinus* spp.) (Steirly 1957, Ligon 1970, Lay 1970). Each Red-cockaded Woodpecker social unit, or group, occupies a cluster of cavity trees, usually containing a number of both active and inactive cavities (Walters 1990). Red-cockaded Woodpeckers maintain a constant flow of sticky resin around active cavities by regularly excavating resin wells in the vicinity of the cavity entrance (Ligon 1970). Also, a smooth tree bole is created by scaling loose bark from the trunk (Ligon 1970, Rudolph et al. 1990a). The resin flows down the smooth trunk of the tree and helps to create a barrier against predation by rat snakes of the genus *Elaphe* (Jackson 1974, Rudolph et al. 1990b).

A number of other species are known to use Red-cockaded Woodpecker cavities with the southern flying squirrel (*Glaucomys volans*) being one of the most frequent users (Baker 1971, Dennis 1971, Hopkins and Lynn 1971, Harlow and Lennartz 1983, Conner et al. 1996). Flying squirrels prefer entrance diameters similar to those preferred by Red-cockaded Woodpeckers, thereby creating the potential for cavity competition (Rudolph et al. 1990a, Loeb 1993). On 19 April 1991, while checking Red-cockaded Woodpecker cavity contents on the Angelina National Forest in eastern Texas, we observed the following southern flying squirrel behavior. Tree A had one inactive cavity containing eight flying squirrels. Tree B had a total of three cavities. The lowest cavity (4.6 m above ground level) was inactive and contained three flying squirrels, while the middle cavity (3 m above the lowest cavity) was inactive and empty. The uppermost cavity (2.4 m above the middle cavity and 0.2 m below the base of the crown) was active and served as the breeding male Red-cockaded Woodpecker's roost cavity, and the group's nest cavity in 1990 and 1991. There was a well developed coating of sticky resin extending from about 0.5 m above to 1.5 m below the cavity. After being flushed from its cavity by our activities, one of the eight flying squirrels from tree A glided to tree B and entered the lower cavity. It immediately exited the lower cavity, presumably expelled by the three flying squirrels already in it, ran up the trunk and entered the middle cavity. Shortly thereafter, a second flying squirrel from tree A repeated the same scenario as the first flying squirrel. Subsequently, during the process of checking the cavity contents of tree B, we flushed the two flying squirrels from the middle cavity. One flying squirrel exited first and ran up the trunk towards the active cavity entrance. It is unknown if the flying squirrel intended to enter the cavity or to bypass it and seek cover in the canopy. As the flying squirrel came into contact with the sticky resin coating beneath the active cavity, it hopped onto and began using primary branches to make its way up and past the level

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of the fresh resin. While it progressed upward, the flying squirrel occasionally landed on the sticky trunk of the pine but quickly moved off of it as it made its way from branch to branch. When the flying squirrel was above the level of fresh resin it returned to the trunk and continued running up the tree. The second flying squirrel flushed from the middle cavity behaved in the same manner as the first one. Both flying squirrels were clearly attempting to avoid contact with the sticky resin. This is our second observation of such flying squirrel behavior. Although we have no detailed notes describing the first observation, the behavior was very similar. To our knowledge, there are no reports in the literature of resin avoidance by southern flying squirrels.

Dennis (1971) and Rudolph and coworkers (1990a) found little evidence that resin prevents intruders other than snakes from entering active Red-cockaded Woodpecker cavities. We have regularly found one or more flying squirrels in active Red-cockaded Woodpecker cavities. We have also observed instances of a flying squirrel gliding from one tree directly to the entrance of an active cavity in a neighboring tree, thus avoiding most resin contact. Without a doubt, flying squirrels are quite capable of entering active Red-cockaded Woodpecker cavities (Rudolph et al. 1990a, Loeb 1993). However, under some circumstances the resin coating can offer some deterrence.

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Migrant bird participation at an army ant swarm in montane Jalisco, Mexico

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ABSTRACT.—The arthropod-flushing behavior of above-ground swarming army ants (tribe Ecitonini) provides Neotropical birds with a unique food resource. The extent to which birds exploit this resource varies geographically, because of the variable swarming behavior of different army ant species and their distributions. During the winter, Neotropical-Nearctic migrant birds may have greater opportunity at higher latitude army ant swarms because of a lack of dominant, obligate ant-following resident birds. Here we report observations of migrant birds foraging at a northern high tropical latitude, high elevation army ant (*Labidus praedator*) swarm. *Received 1 May 1997, accepted 3 Oct. 1997.*

The extent to which different groups of birds exploit the prey-flushing behavior of army ant (*Eciton burchelli* or *Labidus praedator*) swarms in the Neotropics varies with latitude. Bird species that are obligate followers of army ant swarms decrease in frequency northward from the equator, until none occur north of southeastern Oaxaca, on the Pacific slope of Mexico (Willis and Oniki 1978). Only several non-obligate, but "regular," army ant-following species occur farther north (Willis and Oniki 1978). Both obligate and regular army ant-following birds are generally associated with swarms of *E. burchelli* because of that species' predictable and reliable swarming behavior (Willis 1966, 1967; Willis and Oniki 1978). In contrast to *E. burchelli,* above-ground swarming by *L. praedator* is irregular, unpredictable, and generally does not support obligate species of ant-following birds (Willis 1966, 1967; Willis and Oniki 1978). Irregular, facultative foraging by resident and migrant birds, however, frequently occurs at raids of *L. praedator* (Willis 1966, Willis and Oniki 1978), and *E. burchelli* when dominant, obligate ant-following resident birds are absent (see Coates-Estrada and Estrada 1989).

While investigation of bird-army ant interactions has been extensive in the lowland tropics (reviewed in Willis and Oniki 1978, 1992), much less has been reported from northern higher latitudes (Greene et al. 1984, Coates-Estrada and Estrada 1989) and higher elevations. We present observations made on 13 January 1996, at a *L. praedator* raid near Autlan de Navarro, Jalisco, Mexico (19° 46′ N, 104° 22′ W; approximately 1500 m above sea level). Flock composition at this ant raid is of special interest because of the large number of individuals and migrants present. None of the participating species has been previously reported at army ant raids (cf., Willis 1986a, b; Willis and Oniki 1992). Observations from this *L. praedator* raid add to the scarce data regarding facultative foraging by birds at army ant raids in western Mexico, and to the poorly-documented trends of increased migrant participation at raids north of where obligate ant-following birds occur.

The leading edge of the ant swarm was approximately 3 m wide, and moved over the ground through non-deciduous oak (*Quercus* spp.) forest with a closed canopy of 8–10 m in height and little-developed understory. Eight bird species totaling 30 individuals were found to be actively foraging on prey flushed by the activity of the ant swarm. At least five species (25 individuals) were wintering migrants, including Nashville (*Vermivora ruficapilla*), Yellow-rumped (*Dendroica coronata auduboni*), Black-throated Gray (*D. nigrescens*), and Townsend's (*D. townsendi*) warblers, and Bullock's Oriole (*Icterus bullockii*). Two Hepatic (*Piranga flava*) and two Flame-colored (*P. bidentata*) tanagers were likely permanent residents (cf., Howell and Webb 1995). One probable migrant American Kes-

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trel (*Falco sparverius*) was also attending the army ant swarm, but may have been attracted by the presence of the attendant passerines.

Yellow-rumped (Audubon's) Warbler was the most abundant species at the ant raid, with 20 individuals present compared to 1–2 individuals of each of the other attendant species. Unlike all other participants, Yellow-rumped Warbler and American Kestrel were not found in any of the numerous non-army ant-associated mixed-species flocks in the area. Yellow-rumped Warblers foraged vigorously, and close to the ground (< 1 m), staying directly above the area of highest ant activity and perching on small-diameter stems and branches. Nashville, Black-throated Gray, and Townsend's warblers also foraged at the center of ant activity (zone A as described by Willis and Oniki 1978), remaining below 4 m and making frequent attacks to the ground or low foliage near the leading edge of the swarm. Flame-colored and Hepatic tanagers and Bullock's Orioles perched higher in the sub-canopy (4–7 m) and farther from the center of activity (zone B; Willis and Oniki 1978). A lack of dominance by the larger resident participants may have allowed occupancy of the richest area of the swarm by smaller species. The warblers took small insects, including adult moths (Lepidoptera) and Diptera, while the larger species, such as tanagers and orioles, were observed feeding on larger arthropods, including Orthoptera. We did not determine prey items of the American Kestrel, as it retreated from the ant swarm with our approach. It may have been attracted to the birds as much as to the arthropod prey, although many large Orthoptera and scorpions (Arachnida) were observed fleeing the ant raid.

Migrant birds very rarely occur at Amazonian army ant swarms (Willis and Oniki 1978), but may compose up to 30% of ant-following bird flocks at *E. burchelli* raids in Panama (Willis 1966). Based on their observations of 62% migrant composition at an *E. burchelli* raid in Guerrero, Mexico, Greene and coworkers (1984) proposed that migrants may have more opportunities at army ant raids farther north in the absence of aggressive obligate ant-followers.

In the case of *L. praedator* raids, Willis (1966) found migrant participation in Panama to reach 50% during peak fall periods. Our flock in Jalisco was composed of 87% overwintering migrant birds, the highest value reported to date, and represents one of the northernmost records of migrant birds attending an army ant swarm on the Pacific slope (see also Hardy 1974). In addition to the high proportion of migrants, our flock had a very large number of participants. Willis (1966) found a high of only 5.1 migrant individuals (average; 0.2–5.1) at *L. praedator* swarms in Panama. Coates-Estrada and Estrada (1989) reported a mean (±SD) of 1.6 ± 1.5 migrants per *L. praedator* swarm, and 1.9 ± 1.3 per *E. burchelli* swarm, in Veracruz, Mexico. The presence of several "regular" ant-following residents on the eastern slope of Mexico, however, may limit migrant participation at this northern site (Coates-Estrada and Estrada 1989).

In addition to a latitudinal gradient in migrant participation at northern army ant swarms, elevation may also affect migrant accessibility at montane swarms. Increased facultative participation at higher elevation swarms has been described by Hilty (1974) and has been attributed to a similar lack of obligate ant-following bird attendance at higher elevation swarms.

Because of the unreliability of *L. praedator* ant swarms in the highlands of western Mexico, Neotropical migrants probably follow them only opportunistically. Despite this unpredictability, *L. praedator* raids, as well as those of *E. burchelli*, may provide an important occasional resource for migrants. Our observations suggest that bird-army ant interactions at high tropical latitudes are worth attention because of their importance as a sporadic food resource for wintering Neotropical migrants, especially in areas of high migrant density such as western Mexico (see Hutto 1987, 1992).

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Ornithological Literature

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ECOLOGY AND MANAGEMENT OF NEOTROPICAL MIGRATORY BIRDS: A SYNTHESIS AND REVIEW OF CRITICAL ISSUES. Edited by Thomas E. Martin and Deborah M. Finch. Oxford Univ. Press, New York. 1995: 489 pp., numerous tables and figures. $35.00 (paper); $65.00 (cloth).—In the 1970s, two lines of evidence converged to focus the attention of ornithologists on the ecology of migratory songbirds. At about the time that researchers in eastern North America realized that Neotropical migrants had declined precipitously at several widely scattered woodland sites, researchers in Central America and Mexico were discovering that Neotropical migrants are common winter residents in the interior of tropical forests that are melting away with the expansion of human populations. The prospect that many of the most abundant breeding birds in North America might be in trouble triggered hundreds of research projects on the habitat requirements and population ecology of Neotropical migrants. Although the results of these studies have been summarized and synthesized periodically in a series of books and review papers, the rapid pace of research on Neotropical migrants requires new summaries every few years. This volume does an excellent job of integrating and interpreting information from recent research on neotropical migrants.

To prepare this volume, groups of researchers were invited to work together to review the literature on their general areas of interest. The goal was to minimize theoretical and regional bias and ensure that different perspectives were represented. Generally this approach worked well. For example, the chapter on winter habitat use (Daniel Petit et al.) was written by researchers who had studied migrants in the West Indies, the Yucatan Peninsula, western Mexico, and Central America. Because studies from these different regions are compared so thoroughly, the resulting conclusions are robust: Neotropical migrants are found in a wide range of habitats in winter, including early successional and agricultural habitats, but some species are primarily restricted to large areas of undisturbed forest or to specific habitats such as mangrove swamps or pine forests. Similarly, the chapter on the impact of cowbirds on Neotropical migrants (Scott Robinson et al.) is written by researchers who have studied cowbirds in regions with different cowbird densities, host species, and landscape patterns, so regional differences in the effect of cowbirds are emphasized.

Another distinctive feature of this volume is that authors were asked to thoroughly address the implications of research findings for conservation and management of Neotropical migrants. Although the result is useful synthesis for researchers, the main goal was to interpret the scientific literature for foresters, wildlife biologists, and conservationists. Most chapters provide useful advice on management and conservation, but this is usually in the form of general recommendations rather than precise prescriptions of the type that foresters and wildlife managers frequently use for regenerating white pine or managing gamebird populations. For example, in the chapter on silviculture in central and southeastern oak-pine forests, James Dickson and coworkers recommend a mix of selection cutting and even-aged management to maintain both small and large openings and a range of successional stages. They also recommend several methods for preserving large blocks of continuous forest needed by edge-sensitive species: large areas reserved from timber harvest, larger regeneration cuts on longer cutting rotations, or single-tree rather than group selection cuts.

In most chapters, management recommendations flow seamlessly from the analyses of the habitat requirements and behavior of migrants. However, in a chapter on the effects of livestock grazing (Victoria Saab et al.), the general prescription for "large (at least 1000 ha), permanent livestock exclosures" (pg. 342) clearly applies to habitats such as desert grasslands and shrubsteppe where there were few native grazers, but not so obviously to the shortgrass prairie where "millions of native

ungulates (bison) were obliterated and then replaced with millions of exotic ungulates" (pg. 314), and where different species of birds are adapted to grassland in different stages of recovery from grazing.

For both resource managers and researchers, one of the most important chapters concerns whether populations of Neotropical migrants are limited in summer or winter. This is not only a contentious theoretical issue, but also an important practical issue: efforts to manage breeding habitat for migrants in Wisconsin forests or Kansas grasslands will be ineffective if populations are actually limited by availability of suitable wintering habitats thousands of miles to the south. Thomas Sherry and Richard Holmes develop an elegant graphical model which shows how population change probably results from a complex interplay of habitat availability in both summer and winter. This model depends on the assumption (confirmed by several recent studies) that habitat varies in quality in both breeding and wintering areas. If nesting habitat is destroyed, then fewer birds will migrate to the topics during the winter. Consequently, a higher percentage of birds will find favorable winter habitat, increasing the average rate of survival. If winter habitat is destroyed, then fewer birds will return to the north, and a larger proportion of the survivors will settle in the best breeding habitat. Thus, losses at one end of the migratory route will be offset to some extent (and within limits) at the other end. For conservationists, this model implies that local efforts are nearly always worthwhile, but international cooperation is ultimately essential.

Most of the 17 chapters emphasize the importance of considering the regional context of a patch of habitat, regardless of whether the issue is winter habitat, migratory stopover sites (Frank Moore et al.), or breeding areas. The most cohesive discussion of population dynamics at the landscape scale is presented in two chapters that focus on habitat fragmentation. John Faaborg and coworkers emphasize the negative impact of habitat edge, while Kathryn Freemark and coworkers describe how reproductive and surivial rates depend not only on the habitat within and on the edge of a site, but also on the landscape patterns in the larger region around the site.

The initial chapters focus on analysis of data from the Breeding Bird Survey (our main source of information on large-scale population trends) (Bruce Peterjohn et al.) and on methods for conclusively determining the cause of population trends (Frances James and Charles McCulloch). John Rotenberry and coworkers analyze the importance of natural perturbations (fires, storms, insect outbreaks) for Neotropical migrant populations. Other chapters provide comprehensive reviews of the effects of timber harvesting (Frank Thompson III et al., Sallie Hejl et al.), farming (Nicholas Rodenhouse et al.), pesticide contamination (Nicholas Gard and Michael Hooper), and management directed at single species and guilds of species (William Block et al.).

This book will be a logical starting point for anyone planning to manage habitat for migratory birds in a particular region as well as for those interested in understanding the adaptations and requirements of long-distance migrants during the complex yearly cycles. The authors have effectively summarized and interpreted much of what is known about the ecology and conservation of Neotropical migrants.—ROBERT A. ASKINS.

NEOTROPICAL BIRDS: ECOLOGY AND CONSERVATION. By Douglas F. Stotz, John W. Fitzpatrick, Theodore A. Parker III, and Debra K. Moskovits. Univ. of Chicago Press, Chicago, Illinois. 1996: 502 pp., 3 large maps, 16 color plates, 46 black and white plates, 48 numbered text figures (that include small maps), 9 databases. $37.50 (paper); $100 (cloth).—In this ambitious volume the authors attempt to summarize relevant vegetation and physical characteristics of all Neotropical habitats and, more importantly, to provide an overview of the conservation status of each. A major component of the volume is the inclusion of nine databases (also available from the publisher on diskette) that together will prove invaluable to anyone researching Neotropical ornithology. These databases collectively occupy 306 pages, while the main text takes up but 130 pages. As would be expected, there is an extensive literature cited section.

The first part of the book is devoted to five chapters that review avian habitat types, hu-

mid forests, dry forest and arid scrub, grasslands, and aquatic communities. These chapters outline the major threats to birds in each of these habitat types. The surprising conclusion, at least for those who have relatively little actual experience in the Neotropics, is that lowland humid forests, rainforests, are not the habitats facing the most severe threats. Rather, it is dry forests, savannas, and more arid habitats, many of which contain a high percentage of endemic bird species, that are most at risk. For example, in the extensive Brazilian cerrado, a dry woodland of short stature trees that occupies much of southeastern Brazil, the authors suggest that 40% of the endemic bird species are threatened or endangered, while fully three-fourths are considered at risk. Loss of natural cerrado by habitat conversion (as for soybean production) is considered an "unheralded crisis." While each of the chapters is brief, there is much information to be gleaned and all of the chapters are well referenced to the professional literature.

Two chapters provide an overview of migrant birds, one chapter devoted to Nearctic migrants and one to Austral and Intratropical migrants. Regarding Nearctic migrants, the authors assert that population declines resulting from habitat loss in the Neotropics has not been well substantiated and they believe that most species have not declined for this reason. Those migrants most at risk are believed to be those restricted to lowland forests of Central America and the Greater Antilles (where deforestation has been extensive) as well as the pampas grasslands of Patagonia. Most Nearctic migrants occupy pine and pine-oak ecosystems, lowland evergreen forest, secondary forest, and coastal habitats, all ecosystems which are still relatively widely distributed and extensive in area. The chapter on austral migrants and intratropical migrants will prove insightful in demonstrating how common regional movements are. Neotropical bird communities undergo more fluctuation than many realize, and this chapter helps explain some of this intrinsic variability.

The two final chapters are devoted to developing principles for conservation policy and an evaluation of those areas most at risk. The main point is to suggest a concept the authors call "globally significant cornerstone habitats," defined as "regional habitats containing large proportions of the endemics that are restricted to that vegetation type." The concept of endemism is thus used as the fundamental criterion for making decisions about which areas most deserve protection. The logic for this position is well argued. The authors suggest recognizing five stages of threat to bird communities: the ancestral condition (as with the Venezuelan tepuis, not yet threatened); vulnerable communities (few endangered endemics, as with the Gulf-Caribbean Slope and Southern Amazonia); endangered communities (more than 20% of endemics threatened, as with the Brazilian Atlantic Forest and Northern Andes); severely endangered communities (about 60% of endemics threatened or endangered, as with the Lesser Antilles); ecological collapse (as with the Hawaiian Island avifauna—no Neotropical bird communities as yet fit into this category). Overall, threat to an avian community is measured by factoring in total vulnerable species, percentage of avifauna endangered or threatened, percentage of avifauna vulnerable, percentage of endemics at risk, and percentage of habitat–restricted endemics at risk. Using these variables, five ecosystem groups are recognized with regard to level of precariousness.

The nine databases, authored specifically by Theodore A. Parker III, Douglas F. Stotz, and John W. Fizpatrick, provide an immense amount of information and will prove indispensable to researchers. These databases include the following: a huge table (161 pages) containing the zoogeographic and ecological attributes of all Neotropical bird species, the distribution of Neotropical bird species by country; two databases on Nearctic migrants, one on Astral migrants, plus databases on seabirds not breeding in the Neotropics, Nearctic partial migrants, Austral partial migrants, and indicator species. The databases are part of the legacy of the late Ted Parker.

It is hard to image any Neotropical ornithologist who would not find this volume essential. It is a splendid summary of a vast amount of information, much of which requires action in the near future if, indeed, the future of Neotropical bird communities is to be in any way assured. Beyond that, the book contains solidly argued methodological approaches that should prove useful to inform those making conservation decisions.—JOHN C. KRICHER.

LIVES OF NORTH AMERICAN BIRDS. By Kenn Kaufman. Houghton Mifflin, Boston, Massachusetts. 1996: 703 pp., 645 color photographs, 604 color range maps. $35.00 (hardcover).—This could be an extremely short review: "Rush out and get this book. Now!" However, you might want a few good reasons why this frantic suggestion might be justified. This book is a convenient reference to over 900 birds found in North America, with mini-life-histories on 680 of them and shorter accounts on more than 230 others. Curiously, the volume started as a CD-ROM, reversing the "usual" pattern of some book transmogrifying into an electronic form. (Fear not. Atavistic bibliophiles, techno-peasants, and die-hard luddities should still feel quite comfortable with Kenn Kaufman's book. Indeed, we might not have guessed the origins of this book unless Kaufman himself had let us in on the story in the volume's Acknowledgments.)

The book's species treatments are divided into long and short versions—hereafter called "the full treatments" and "the brief treatments" respectively.

The full treatments cover an introduction to the species (usually dominated by a general description, characteristic behavior, and interesting history on the species in North America), habitat preference, feeding (activity and diet), nesting (territorial display, nest, eggs, incubation, and care of young), migration, and conservation status. Except for the first two categories—the introduction and habitat—you cannot find this information in standard field guides (the recent Stokes' admirable contribution to the genre notwithstanding). I particularly appreciated Kaufman's insightful sections on "Nesting," providing fine short summaries of each species' breeding biology. The "Migration" sections are also creative and enlightening, covering range, usual movements, dispersal, and irruptions. The sections on "Conservation Status" are excellent, especially these days with growing interest in and sensitivity toward such species as Neotropical migrant forest birds and grassland species.

A full treatment will also have a photo and, usually, a range map for each species. However, I would not recommend buying the book simply for these two elements. The maps are small and only give a general idea of North American bird distribution. The photos are normally good, but there are some small or dark notable exceptions, particularly among the Procellariiformes [e.g., Black-capped Petrel (*Pterodroma hasitata*), Buller's Shearwater (*Puffinus bulleri*), Leach's Storm-petrel (*Oceanodroma leucorhoa*), and Ashy Storm-petrel (*Oceanodroma homochroa*)]. Moreover, the photos have no captions to indicate the time and location of the shot, a point of importance to many serious bird students.

The brief treatments are exactly that, with over 230 species typically getting no more than four sentences on their natural history and North American status. Kaufman included every single unusual species that I sought in his brief treatments [e.g., Little Shearwater (*Puffinus assimilis*), Paint-billed Crake (*Neocrex erythrops*), Large-billed Tern (*Phaetusa simplex*) and Pine Bunting (*Emberiza leucocephalos*)]. They all were there.

Nonetheless, what is perplexing to this reviewer were Kaufman's standards for choosing which species would get the full treatments and which ones would get the brief treatments. While I originally thought that Kaufman was providing the full treatments for all North American breeders—justifying the fine nesting section in each full treatment—I shortly found out that this could not be so. Such non-breeders in North America as White-tailed Tropicbird (*Phaethon lepturus*), Short-tailed Shearwater (*Puffinus tenuirostris*), South Polar Skua (*Catharcacta maccormicki*), and Brown Booby (*Sula leucogaster*) all got full treatments. These species may breed in the Caribbean, Australia, Antarctica, and Mexico, respectively, but not in North America. Contrariwise, some North American breeders only got brief treatments.

Why would Kaufman give full treatment to such breeders as Curlew Sandpiper (*Calidris ferruginea*) but not Wood Sandpiper (*Tringa glareola*), Ruff (*Philomachus pugnax*) but not Mongolian Plover (*Charadrius mongolus*), White Wagtail (*Motacilla alba*) but not Red-throated Pipit (*Anthus cervinus*), Spotted Dove (*Streptopelia chinensis*) but not Crested Myna (*Acridotheres cristatellus*), Buff-collared Nightjar (*Caprimulgus ridgwayi*) but not Antillean Nighthawk (*Chordeiles gundlachii*),

Yellow-green Vireo (*Vireo flavoviridis* but not Streak-backed Oriole (*Icterus pustulatus*)?

Alas, not one parrot is given a full treatment.

These inconsistencies notwithstanding, the treatments—full or brief—are nothing short of superb. The book is simply packed with information, ready to burst like some ornithological bouillon cube.

I would be remiss if I did not mention the book's wonderful Introduction, explaining the organization of the book and the organization of the species accounts. It is thorough, informative, and interesting, yet, surprisingly, neither technical nor simplistic. The Introduction contains the words of an author who is clearly familiar and comfortable with his subject. In the Introduction, moreover, Kaufman challenges the inquisitive field birder to add to ornithological knowledge, drawing attention to what we *don't* know about birds.

And, in the same area of arcane knowledge, I tried to "catch" Kaufman on some very obscure incubation periods and nestling periods for scores of species. I only succeeded a half-dozen times, and these were, I stress, some very obscure species [e.g., White-tipped Dove (*Leptotila verreauxi*), Red-whiskered Bulbul (*Pycnonotus jocosus*), Sprague's Pipit (*Anthus spragueii*), and Rufous-winged Sparrow (*Aimophila carpalis*)].

Finally, are there reasons why you wouldn't want this book?

The most serious ornithological researcher would be disappointed with the lack of detailed references. But Kaufman freely admits that including this information within the full and brief treatments would have made his text—designed for a general, though curious, audience—unwieldy. Besides, the professional ornithological camp has the fully adequate *Birds of North America,* though without the sprinkling of the Kaufman charm.

In brief, there is no good reason *not* to buy this work. Kaufman wished to focus on "keeping everything as clear and accessible as possible," and he has succeeded admirably. The book is instructive, engaging, and surprisingly compact. Yes, I was probably right the first time: "Rush out and get this book. Now!"—PAUL J. BAICICH.

HANDBOOK OF AUSTRALIAN, NEW ZEALAND & ANTARCTIC BIRDS, VOLUME 3 SNIPE TO PIGEONS. Edited by P. J. Higgins and S. J. J. F. Davies. Color illus. by J. N. Davies. Oxford University Press, Melbourne, Australia. 1996: 1028 pp., 60 color plates, numerous maps, sonagrams, and line drawings. $265 (cloth).—This third volume of this mammoth project produced by the Royal Australasian Ornithologists Union covers the remainder (eight families were covered in Volume 2) of the Charadriiformes—the Scolopacidae (sandpipers and allies), Glareolidae (coursers and pratincoles), and Laridae (skuas, jaegers, gulls, and terns)—and the Columbiformes (Columbidea, pigeons and doves). The nomenclature and taxonomy generally follow Christidis and Boles (1994. RAOU Monogr., 2). Family and subfamily account introduce the 129 species accounts. The species accounts typically have sections on field identification (including a section on similar species), habitat, distribution and population, movements (including long-distance banding recoveries and banding summaries), food, voice, plumages and bare parts, molts, measurements, structure (e.g., wings long, narrow and pointed), ageing, and geographical variation for migratory species not breeding in the handbook area. Sections on social organization and behavior, and breeding are added, where appropriate, for breeding species. Diagrams delineating breeding season, present in volumes 1 and 2, are not present in volume 3. Maps show confirmed breeding areas in red, with areas where the species occurs but breeding has not been ascertained in half-tone red. For migratory species a world map showing breeding distribution supplements detailed distribution in the handbook region. The species accounts appropriately are of different length, ranging from a page or two for vagrants to nearly 30 pages for some gull species. The color plates are generally good quality, but I like the plates of pigeons and doves better than those of shorebirds.

I could not help but be impressed with how little is known about a large percentage of the species covered. Among the pigeons and doves, for example, for even widely distributed species like the Diamond Dove (*Geopelia cuneata*) the BREEDING section begins "Not well known, no major studies"; in the

Bar-shouldered Dove (*G. humeralis*) it begins "Poorly known, no major studies"; in the Emerald Dove (*Chalcophaps indica*) "Not well known, no major studies". In the Pacific Gull (*Larus pacificus*), a species endemic to southern Australia, we find MOVEMENTS "Poorly known"; SOCIAL ORGANIZATION "Poorly Known"; SOCIAL BEHAVIOUR "Poorly known; no published studies"; VOICE "Poorly known, No detailed studies"; BREEDING "Poorly known, no major studies"; GEOGRAPHICAL VARIATION "Poorly known". Clearly, one of the major contributions of this handbook series will be its heuristic value. Detailing what is not known may in the long run be more valuable than detailing what is known.

The book has a few minor problems. The printing in volume 1 was much easier to read than in either vol 2 or 3. I am also bothered by the lack of social interaction and breeding information on birds that only winter in the region covered by the handbook. Certainly, simply because a bird doesn't breed in an area doesn't preclude an interest in its breeding biology. At least a brief summary and references would have added a more cosmopolitan dimension to the work, and justified the expense of the added pages.

There are a number of features which I particularly like. The color descriptions are intelligible to non-specialists who may be unfamiliar with "burnt umber" but can picture "dark brown." The type-face is the same size throughout the accounts, letting the reader decide what should be considered more or less important. By far my favorite feature is the inclusion of references at the end of each order, family, subfamily, and species account. This is a very "user-friendly" feature, especially if you want to photocopy a particular account.

Overall this is an excellent contribution. The accounts are well researched, the illustrations generally adequate for coverage of sex and age differences in plumage, the book is well laid out and sturdy. The series is **the** source for quickly and easily finding what is known (and not known) about birds in the Australasian region. The price may well be prohibitive for most individuals, but is essential for any serious student of birds of this region. Hence it is a must for academic libraries.—WILLIAM E. DAVIS, JR.

THE HISTORICAL ATLAS OF BREEDING BIRDS IN BRITAIN AND IRELAND: 1875–1900. Compiled by Simon Holloway. 1996. T & AD Poyser, London, UK. (United States Edition by Academic Press, Inc., San Diego, California). $39.95.—The late Trevor Poyser's legacy to the ornithological world was the magnificent series of books bearing the imprint of T & AD Poyser, primarily species monographs but with a number of subject monographs, including the three atlases of Britain and Ireland (*The Atlas of Breeding Birds in Britain and Ireland* (1976), *The Atlas of Wintering Birds in Britain and Ireland* (1986), and *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991* (1993)). The volume under review constitutes the fourth atlas, this time not an atlas of contemporary distributions but a compilation of historical records for the last quarter of the Nineteenth Century. Despite this, Holloway is eminently readable: science and natural history, not the dry facts of history, leap from these pages.

In 1852 Hewett Cottrell Watson (1804–1881), a noted English amateur botanist of the Nineteenth Century, gave a list of 38 subprovinces and 112 "vice-counties" into which he proposed to divide Britain so as to provide a set of geographical units more equal in their areas than were the political counties. With this advent of the Watsonian vice-counties was laid the foundation for a relatively systematic recording format in Britain (and in Ireland, where county sizes were, with two exceptions, more uniform in size). Watson's vice-counties provided the means for systematic recording of the distribution of plants and animals throughout the two islands, this eventually yielding to the 10 km grid squares of the three modern atlases but allowing the present compilation almost comparable comprehensiveness for data 100 years older!

Holloway's volume begins with a general introduction outlining the historical background to the period and providing details of the vice-county system. A 14 page section on his data sources follow. In addition to the three major Eighteenth Century avifaunas covering Britain and Ireland and associated with the names Yarrell, Thompson, and More, Holloway consulted more than 100 county and regional avifaunas for the period 1875–

1900. Geographic details are provided for each of these, together with a short paragraph about the authors of these works. Glancing through the biographies of these authors is fascinating, revealing much of the sociology of late Nineteenth Century ornithology and providing insight as to the origins of the wealth of avifaunas for England compared to the paucity for North America for the same period. Clergymen feature prominently, reflecting the triplet of an assured stipend from the Church of England, time on their hands, and natural history as a suitable occupation for a clergyman. However, lawyers, school teachers, academics, bankers, soldiers, nurserymen, and other occupations appear in these accounts, together with the obligatory dozen or so of independently wealthy English gentlemen. These accounts provide a fascinating glimpse of the nature of the world of ornithologists at that time and their inclusion here is a touch of genius on Holloway's part. A 10 page section follows to describe the late Nineteenth Century environment in relation to habitats and land use changes. In contrast to the primary sources used extensively for the historical information on birds, this section is based primarily on secondary sources, with heavy reliance on, for example, Marchants and coworkers' (1990) *Population Trends in British Breeding Birds* (British Trust for Ornithology, Tring) and Fuller's (1982) *Bird Habitats in Britain* (Poyser, Calton) for information as to how various land changes impacted bird populations.

A short 3 page section introduces the species accounts, primarily describing the layout of the accounts. The main point of interest here is Holloway's procedure for standardizing the abundance scores for each species. The authors of the Nineteenth Century avifaunas used language very differently one from another, so that such phrases as "not uncommon" are likely to mean different things for a given species in different regions. To standardize the historical picture in the face of such variation, Holloway painstakingly collated the descriptions from each avifauna, so that within each the spread in terminology from species known to be extremely rare through to those known to be abundant was, in effect, rank ordered, and this ordering was then standardized across avifaunas.

Each major account consists of two facing pages. On each 2 column text page the species' name and a woodcut illustration from Yarrell's (1837–1843) *A History of British Birds* precede the text account describing the status of the species in Britain and Ireland in the final quarter of the Nineteenth Century, concluding with a brief summary of the current distribution as revealed by the modern atlases. A nice touch for each species title is the inclusion after the current English name of older names that were at one stage widespread in use. One forgets just how recently such names as Land Rail for the Corncrake *Crex crex,* Waterhen for the Moorhen *Gallinula chloropus,* and Ring Dove for the Woodpigeon *Columba palumbus,* have fallen into disuse. At the bottom of each page is (in most cases) a small table showing the numbers of British and Irish counties of breeding (probable, confirmed, and combined) in 1875–1900 and in 1968–1972 (the dates of 1976 *Atlas of Breeding Birds*), and the proportional changes involved. Here the unwary reader may be caught by the occasional references to a 34-county Ireland (rather than to the 32 political counties), this is because Galway and Tipperary were each divided in two since Nineteenth Century data were regularly available for these two sub-counties. Occasionally the structure of this table is changed somewhat, by necessity. Thus, for the Gannet, *Morus bassanus,* it is the number of colonies and number of pairs for the periods 1900 and 1984–1988 that are recorded. Similarly for the Red Kite, *Milvus milvus* (now restricted to a single region in Wales), and for the White-tailed Sea Eagle, *Haliaeetus albicilla* (now extinct), these tables are omitted altogether. Some species accounts depart from this standard format. For the Tufted Duck, *Athya fuligula,* the text includes a map showing the extension of the breeding range of this species in Scotland during the Nineteenth Century; for the Scaup, *Aythya marila,* a table showing the dozen or so occurrences of Twentieth Century breeding at locations in Scotland, together with notes as to the breeding effort involved, is provided. For the Common Scoter, *Melanitta nigra,* a graph shows the number of pairs breeding on Lough Erne in Ireland over the period 1909–

1990. Similar variants appear within other species accounts.

In each species account the facing page contains a map with each vice-county (or in Scotland a faunal region) shaded to indicate one of seven classes of abundance (not breeding, probable but not confirmed, occasional, rare, uncommon, common, and abundant). An eighth category, extinction, is indicated where appropriate by the letter "E" being positioned in the vice-county or vice-counties. For island-breeding seabirds the locations of the islands are indicated by large dots of the appropriate color, while for coastal-nesting seabirds such as the Cormorant, *Phalacrocorax carbo,* or the Kittiwake, *Rissa tridactyla,* a color band along the coastal margin of the vice-county is used to indicate status. In the top righthand corner is reproduced (rather poorly) the dot distribution maps from the 1968–1972 *Atlas of Breeding Birds* (though I have yet to find a statement anywhere in the book that this is where these maps came from).

The 149 main species accounts are followed by brief (2–3 per page) accounts of other species that have bred since 1800 but not during 1875–1900, together with the species that colonized Britain or Ireland in the Twentieth Century but that were never recorded breeding during the Nineteenth Century. A short appendix provides historical details on the avifauna of various small islands around Britain and Ireland, these islands often having been the subject of particular accounts during the Nineteenth Century. Finally, three appendices list the names and scientific names of plants, birds, and other animals mentioned in the text, followed by a 13-page bibliography, an acknowledgments section, and an index of bird names.

A small number of errors have made it through the checking and production process. The introduction to the species accounts refers to the accounts being presented in three sections in taxonomic order, apparently intended to be sections on all species respectively that had bred in Britain and Ireland during 1875–1900; on introduced or domesticated species or those derived largely from such introductions or human intervention; and on other species. However, the first two of these appear to have been merged in the book, this introduction notwithstanding. As noted above, the reproductions of the original *Atlas of Breeding Birds* dot distribution maps appears to be unacknowledged, and it also took me awhile to find the information about the provenance of the woodcuts used in each species account. The citation to Hulme (1984) on page 34 is not accompanied by a corresponding entry in the bibliography, a reference on page 36 to "Beswick" should be to Thomas Bewick, and the entry for the *Atlas of Winter Birds* in the bibliography on page 463 is described as the "*Atlas of Winering Birds*"! On page 96 the graph is indicated as referring to the period 1905–1900, instead of correctly 1905–1990. With these few exceptions, the text otherwise seems to conform admirably to the high standards set by Poyser for his imprint.

The book will appeal to two groups of North American ornithologists. First, for those who have ever enjoyed Audubon's diaries or who have read Whitney's (1994) *From Coastal Wilderness to Fruited Plain* (New York, Cambridge Univ. Press), this book is worth a couple of hours' browsing, if only with a library copy. The contrast with North America in the sociology of ornithology, the *tour de force* of a systematic mapping of distributions of these species *in the last century,* and the contrast it provides for North American ornithology is worth the time. A second group of readers probably lies among conservation biologists: there is much empirical data in this work for evaluating ideas about range changes, extinction rates, and so on, on a scale not readily available elsewhere. The data here provide an interesting set of templates against which to evaluate some of the most contemporary ideas in conservation biology. However, for North American readers perhaps the most thought-provoking question raised by this book's existence is the following: how likely is it that in the year 2096 a future writer would be able to produce the equivalent compilation for North America for the closing quarter of the *present* century? I am not sure that such an undertaking will be as feasible as one might first think, and this book may well have some important lessons for us as to how we do our bird recording as the Twentieth Century draws to a close.—RAYMOND J. O'CONNOR.

FIELD GUIDE TO THE BIRDS OF THE MIDDLE EAST. By R. F. Porter, S. Christensen, P. Schiermacker-Hanses, illus. by A. Birch, J. Gale, M. Langman, and B. Small. T & A D Poyser, London. 1996: 460 pp., 112 color plates, maps of distribution. £29.95 (cloth).—The Middle East is an attractive place for birdwatchers. At the meeting spot of three continents, this area is rich in avifaunas with many rare and endangered species, flocks of millions of birds in passage, and thousands of wintering birds. A team of three authors and four illustrators who have extensive ornithological experience in the Middle East countries prepared a field guide which should not be missed by anyone interested in birds of this region. This up-to-date guide describes all species recorded as of the beginning of 1996, and accurate relatively large-sized maps show distribution of each breeding species in detail. A few introductory pages open this field guide, and are followed by 112 color plates of superb quality. Where it is relevant, a range of plumages by age, sex, and geographical variation of that species is shown. Even though there are several species on each plate, the illustrations still depict details with accuracy. Most of the non-passerines and some groups of passerines, such as martins and swallows, wheatears, crows, and finches are portrayed in flight, showing the typical features that help with identification. On the facing page of each color plate are the maps of distribution, and brief descriptions of status and habitat. An identification text of different length for each of the 722 species reflects the multiple-year field expertise of the authors. Written with clarity, this field guide describes the species' appearance and typical behavior. In most accounts, the authors make a comparison with similar species. Description of important identification features and differences between similar species are printed in italics which help with quick utilization of the text. Body length, wing span, and description of voice is included for each species. The book closes with a list of references for each country, a species list, and indices of English and scientific names.

This excellent book is a must for anyone going to this region. Beginners will find it easy to use and learn from. Advanced birdwatchers will learn something new that will ultimately help with correct identification. The bottom line is: this is the best field guide published so far on birds of the Middle East.—JOSEF KREN.

A FIELD GUIDE TO BIRDS OF ARMENIA. By M. S. Adamian, and D. Klem. American University of Armenia, Oakland, CA. 1997: 220 pp., 61 color plates, 348 maps of distribution. $39 (field cover), $44 (hardcover).—Armenia, a country of the size of Maryland that lies in the Caucas mountains between Europe and Asia, has a rich avifauna of 349 species. As part of the former Soviet Union, Armenia birds were included in a few general handbooks, and one work on Armenian birds was published in the 1950s. Shortly after Armenia declared its independence in 1991 an international team of ornithologists began a work on 3-year project, resulting is this splendid field guide. The book opens with a general introduction. Descriptions of bird topography and habitats, basics of bird identification and keeping field records, and how to use the field guide are provided on 20 pages. These introductory chapters target beginners; advanced ornithologists will most likely appreciate a short chapter on habitats of Armenia. The major part of this field guide is species description with color plates on the facing page. English common names follow names given by Sibley and Monroe (1990), however, the sequence of species follows Peters' (1934–1987) classification. For every species a total length, wing span, status regarding seasonal occurrence, and abundance category is provided at the beginning of the account. Identification features, description of similar species (where applicable), behavior, habitat, food, nest, and eggs complete the species account. The species identification features are short but well described, with key features being underlined. I did not find the sections on food, nest, and eggs particularly essential for this type of book. Instead, a more thorough description of habitats and chronology of seasonal occurrence would be more useful. The color plates, a work of 11 prominent, mostly British artists are excellent. They depict an adult individual of each species in different plumages, in many cases juveniles, and where

relevant also subspecies. Partial figures showing key identification features are included in some species. In each illustration, lines point to diagnostic characteristics. The illustrations are larger than illustrations in most field guides. I found the last part of the field guide (as other ornithologists may too) the most appealing. Accurate, four-colored maps show distribution and abundance of each species. They are based on records from the past 45 years, and provide a valuable source of data for larger-scale monographs. In summary, the reviewed field guide is a significant contribution to the so far poorly studied avifauna of Transcausia. Not only ornithologists visiting Armenia, but also surrounding countries, will find it necessary; I highly recommend it.—JOSEF KREN.

HOST-PARASITE EVOLUTION. GENERAL PRINCIPLES AND AVIAN MODELS. Edited by Dale H. Clayton and Janice Moore. Oxford Univ. Press, Oxford, UK. 1997: 473 pp., many figures in text. $45.00 (paper); $110.00 (cloth).—The principles of parasitology offer us the world in microcosm, but managing to integrate the appreciable taxonomic range of parasites and the virtually endless range of hosts is daunting. The seventeen reviews in the volume edited by Clayton and Moore are less daunting, in that the range of hosts is limited to birds. The emphasis is on the evolution of host-parasite interactions, which is an excellent approach to contemporary work in parasitology.

Readers whose exposure to parasitology has been classical, that is, earlier than 15 years ago, will find a virtually new field of study exposed here. Although taxonomy of parasites and the laboratory techniques of study are as important as ever before, the questions posed and the way answers are pursued are clearly taken from the developing field of evolutionary ecology. This places the emphasis on the dynamics of host-parasite interactions. Thus, host-parasite coevolution, sexual selection mediated by parasites, and variation in parasitic virulence are prominent foci of inquiry in this book.

Because the range of topical coverage is restricted to birds, Clayton and Moore point out that avian parasitology has had a lengthy and diverse history. Such history provides a good foundation on which to examine phenomena such as coevolution, coadaptation, and cospeciation, among others that are currently of interest to theorists.

The book consists of three parts. Part I concerns general principles, and includes examination of natural selection by parasites, the genetics of host immune defenses by means of endocrines, behavior, and life-history variation, demographics of parasitized host populations, parasites and bird conservation, host-parasite community ecology, and host-parasite cospeciation.

Part II examines some avian models—birds serving as habitats for viruses, bacteria, fungi, protozoans, helminths, and arthropods, as well as foster parents in brood parasitism (the latter review, by Robert Payne, is the most strictly ornithological of all in the book, and is the most mature and comprehensive review of brood parasitism ever done). Moore and Clayton summarize Part II with an essay on the evolution of host-parasite interactions.

Part III consists of appendices in which techniques of collection and identification of avian parasites are summarized. Indexes to organisms and to topics are adequate, although some organisms with two or more vernacular names have them treated as though they are distinct [e.g., rock dove, rock pigeon, and domestic pigeon (*Columba livia* is not included); if you don't look up all three, you will miss some page references].

This is a serious book with a high level of intent and of accomplishment. Professionals working in ornithology, parasitology, and evolutionary ecology need to have this book, and it should be in all research libraries.—RICHARD F. JOHNSTON.

FLIGHT-FEATHER MOLT PATTERNS AND AGE IN NORTH AMERICAN OWLS. By Peter Pyle. American Birding Association Monographs in Field Ornithology No. 2, 1997: 32 pp., 14 figs. 8½″ × 11″, heavy paper cover, spiral-bound. $9.95.—According to the author, "molt schemes in several species [of North American owls] have been erroneously reported or are underdescribed, and for other

species accurate information exists but its full applicability for ageing has not been examined." Several papers that misinterpreted owl molts and the presence of more than one generation of flight feathers are cited. The author's goal was to clear up the misunderstandings and provide an accurate account of owl molts and plumages with the emphasis on ageing birds in the hand. In this connection he examined 2429 owl specimens from four collections in California. Species samples ranged from 23 for the Boreal Owl (*Aegolius funereus*) to 251 for the Burrowing Owl ["*Speotyto*" (=*Athene,* reviewer's preference)] *cunicularia.* Using body plumage and flight feathers, specimens were assigned age codes using the calendar-based system of the Bird Banding Laboratory, from HY (=hatching year) all the way up (in some instances) to 4Y/5Y (=birds in their fourth basic plumage). The author emphasizes that all assigned ages except for those of obvious juveniles were inferred rather than absolutely known, as older known-age specimens were not available. He recommends that his conclusions be checked against captive [risky—KCP] and recaptured known-aged wild birds.

Conclusions about age were drawn primarily on the basis of active molt plus relative wear of flight feathers. In some species the shapes of particular unworn feathers and also their color patterns can be used in determining age. Full renewal of all primaries and secondaries is said to take as much as six (or more) years in some species; if this is true, the author quite properly asks why replacement of these feathers occurs so slowly in relation to most other birds. He also wonders what, if any, might be the systematic implications of molt patterns in owls. Certainly the identical molt regimes in "*Speotyto*" and *Athene* could be considered evidence for the relumping of these genera.

In his Conclusions section, Pyle states that "Reliable ageing of owls . . . requires caution and experience in many cases. In many owls, molt patterns may not be easily distinguished without practice . . ." Amen! Pyle's findings were based on examination of museum study skins. In trying to age randomly selected owl skins in the collection of Carnegie Museum of Natural History, I found that identifying the individual remiges on the closed wing of study skins was difficult, and trying to assign each to a feather generation based on wear was for me almost impossible. We have a large collection of detached spread wings; using these I had no trouble identifying individual remiges, but without having Pyle's experienced eyes, I could, in general, distinguish only three kinds of remiges: growing, very worn and bleached, and everything else. Differences in shape and pattern were somewhat easier to detect, but did not always fall into the neat categories shown in the drawings. Pyle warns (p. 9) that there is overlap between age groups in these characters.

I believe Pyle's conclusions are probably reasonably accurate, especially considering his caution in their presentation. However, I find myself asking two questions about this publication. First, what is the intended audience? With the inherent difficulty in using conventional study skins, I doubt whether many curators will wish to age their specimens retroactively. Obviously the keys and descriptions will be best used with birds in the hand, whether in general banding projects or in population studies of a particular species when the birds can be captured for ageing. People carrying on such studies are likely to be the only ones willing to pay ten bucks for the publication (other than bird book collectors who buy *everything*). This brings up the second question—why was this paper (for that is really what it is, not a book) published as the second "Monograph in Field Ornithology" of the American Birding Association? Pyle's results are of use *only* with birds in the hand, whereas the emphasis within the A.B.A. has always been on *field identification,* whether simply to species or to age and sex classes. I could easily see this as a paper that the Bird Banding Office might have published for its own audience and anybody else who might be interested, but it doesn't strike me as relevant for the A.B.A. as we know it.—KENNETH C. PARKES.

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A DESCRIPTION OF THE FIRST LIVE POOULI CAPTURED

PAUL E. BAKER[1,2]

ABSTRACT.—The Poouli (*Melamprosops phaeosoma*) is an endangered Hawaiian honeycreeper found only on Maui, Hawaii. It was rare at the time of its discovery in 1973, but by 1997 was on the brink of extinction with fewer than six individuals left. Two specimens were collected for the description of the species, but both proved to be immature by comparison with a pair of adults at a nest. Until 1997 no Poouli had ever been captured alive, and consequently descriptions of adult Poouli were produced from field observations. In 1997, I captured an adult male Poouli which is described here for the first time. Detailed comparisons of the plumage of this adult with that of an immature specimen and previous descriptions of the species are discussed in this paper, as are differences in plumage between adult and immature males and females that may aid the sexing and ageing of birds in the field. *Received 23 August 1997, accepted 17 March 1998.*

Discovered in 1973, the Poouli (*Melamprosops phaeosoma*; pronounced Po-oh-oo-lee) is a critically endangered Hawaiian honeycreeper found only at high elevation on northeastern Maui. Little is known about this elusive species (Engilis et al. 1996, Kepler et al. 1996). Two hatch-year birds were collected, preserved as specimens, and described in 1973 (Casey and Jacobi 1974), but the only descriptions of adult birds are from field observations (Engilis et al. 1996).

Between December 1995–May 1997, members of the Maui Critically Endangered Species Project studied the ecology of the Poouli in the Hanawi Natural Area Reserve, east Maui. This research involved banding of Poouli, but my early attempts at capturing Poouli failed because of their rarity. I often observed Poouli associated with Maui Parrotbill (*Pseudonestor xanthophrys*), so I captured, banded, and released Maui Parrotbill to determine with which individuals Poouli were associating.

METHODS

On 15 January 1997, while on a ridge at 1700 m elevation in Unit 3 of the reserve, I heard a pair of Maui Parrotbill approaching me. I set up one 6 m mist net and used playback of Maui Parrotbill calls and song to lure the birds to the net. The female Maui Parrotbill approached the net with an adult male Poouli close behind. The Poouli disappeared among the foliage in a nearby ohia (*Metrosideros polymorpha*) tree, but the Maui Parrotbill flew away. A minute later the Poouli reappeared in the same tree and flew straight into the mist net. This was the first Poouli ever captured.

I measured maximum leg width to determine band size, then banded the bird with both a US Fish and Wildlife Service metal band and plastic color bands for later field identification. I took standard biometrical measurements of maximum unflattened wing chord, exposed culmen, tarso-metatarsus, and tail as described by Pyle and coworkers (1987). I also recorded bill

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←

FRONTISPIECE. Dorsal and lateral view of plumage of adult male Poouli.

width and depth at the edge of the nostrils nearest the skull, skull length measured from the back of the head to the bill tip, and mass (g). I noted plumage and soft part colors following a morphology list designed by H. Baker for general field and museum use and the recommended format used for plumage description in Birds of North America species accounts, with colors from Smithe (1975). I then photographed and released the bird.

No detailed descriptions of the museum specimens of Poouli have been made, although Casey and Jacobi (1974) and Engilis and coworkers (1996) gave a good generalized description. I examined the holotype Poouli specimen (# 147112) in the Bishop Museum, Honolulu, collected 17 September 1973, and made a detailed description for comparison with the live bird (adult male). The holotype has been kept in a closed drawer in a specimen tray since its preparation, to minimize fading.

RESULTS

Morphometrics of live bird: Band size 1B was best fit. Age and sex: Adult male. Sex was determined by plumage characteristics (Casey and Jacobi 1974; Engilis et al. 1996, pers. obs.), and by observation of the bird's behavior, which included presenting nesting material to a female Maui Parrotbill. Breeding status: I examined the bird for the presence of either cloacal swelling or a brood patch and determined that the bird was not breeding. Wing length: 72 mm. Exposed culmen: 15.32 mm. Bill depth: 7.61 mm. Bill width: 6.33 mm. Skull length: 34.13 mm. Tarsus length: 24.92 mm. Tail length: 36 mm. Mass: 26.2 g. No body fat, lesions, food in crop, or molt. Some wear of remiges and rectrices, but not heavy. Figures 1 and 2 show the plumage of the adult male Poouli.

Plumage description of adult male Poouli (taken from the live bird in the field): forehead, supercilium, eyeline, lores, and narials: Jet Black (89). Crown: Glaucous (79) with feathers at front more Light Neutral Gray (85). Nape: Grayish Horn Color (91). Rictals: None. Rictal flanges: Blackish Neutral Gray (82). Upper back: mix of Glaucous (79) and Raw Umber (123). Lower back and rump: Raw Umber (123). Scapular: Sepia (119) with Hair Brown (119A) edging. Uppertail coverts: Verona Brown (223B) with hints of Antique Brown (37) and Raw Sienna (136). Rectrices: ground color Sepia (119), edged with Verona Brown (223B) with hints of Antique Brown (37) and Raw Sienna (136). Undertail coverts and crurals: Cinnamon (39). Vent: Pale Horn Color (92). Foremost flank feathers: pale grayish off-white ground color, overlain by dirty Pale Horn Color (92) and pale Tawny Olive (223D). Rearmost flank feathers: dark version of Cinnamon (39). Belly: pale grayish off-white ground color, overlain by dirty Pale Horn Color (92). Breast: Smoke Gray (44). Throat: lower throat white, upper throat and chin: Jet Black (89). Auricular: white, almost forming a complete collar round the back of the neck where it fades into pale gray. Malar: Jet Black (89). Lesser coverts: Sepia (119) with Hair Brown (119A), and edged with Grayish Horn Color (91). Alula, median, carpal, and primary coverts: Sepia (119) with Hair Brown (119A) edging. Greater coverts, primaries, secondaries, and tertials: Sepia (119) with Raw Umber (123) edging. Wing lining: dirty Smoke Gray (44). Underside of flight feathers dirty silvery gray.

Description of soft parts: Iris: Mars Brown (223A)–Verona Brown (223B). Ring of skin around eye, culmen, maxilla tomium, maxilla, mandible, mandibular tomium, and gonys: Blackish Neutral Gray (82). Tongue, inside of mouth, and bill: Pink (7). Legs and toes: Warm Sepia (221A). Claws: Sepia (219). Pads of feet: Warm Buff (118).

Plumage description of immature Poouli (holotype) for comparison (taken from specimen): Forehead: dull brown-black not as intense as Jet Black (89), with Dark Drab (119B) tips. Crown: darker Olive-Brown (28) with feathers at front Dark Drab (119B). Nape: richer version of Olive-Brown (28) with tone of Prout's Brown (121A). Supercilium: a dark, richer version of Sepia (119), with Dark Drab (119B) tips. Eyeline: a dark, richer version of Sepia (119) with Dark Drab (119B) tips. Lores: dull black with Dark Drab (119B) tips. Narials: Drab Gray (119D) to off-white. Rictals: None. Rictal flanges: Blackish Neutral Gray (82). Upper back: darker Prout's Brown (121A). Lower back: Cinnamon Brown (33). Scapular: darker Prout's Brown (121A). Rump and undertail coverts: Cinnamon (123A). Uppertail coverts: Warm Sepia (221A). Rectrices: darker Prout's Brown (121A). Vent, crurals, and foremost flank feathers: pale Tawny Olive (223D). Rearmost flank feathers: Cinnamon (123A). Belly: paler version of Tawny Olive (223D) than around

crurals and vent. Breast: upper breast Drab Gray (119D). Shoulders: brownish Drab Gray (119D). Throat: upper throat mix of Sepia (119) feathers and lower Drab Gray (119D) feathers tipped with Cinnamon-Brown (33). Chin: Mix of Sepia (119) feathers and Cinnamon-Brown (33) tipped feathers. Auricular: upper feathers dark Grayish Brown (20), lower feathers pale Tawny Olive (223D). Malar: pale Tawny Olive (223D). Lesser, median, greater, and carpal coverts: a warmer brown version of Prout's Brown (121A). Primary coverts and alula: Vandyke Brown (121). Primaries: basic Fuscous (21), edged with Army Brown (219B). Secondaries and tertials: basic Fuscous (21), edged with Prout's Brown (121A). Wing lining: Difficult to examine, seemed off-white with heavy wash of pale Tawny Olive (223D).

Description of soft parts: Iris: dark brown (Casey and Jacobi 1973). Ring of skin round eye: no information. Culmen, maxilla, mandible, and tomia: almost Jet Black (89); darker than Blackish Neutral Gray (82). Gonys: tip Pale Horn Color (92). Tongue: no information. Inside of mouth and bill: no information. Legs and toes: Natal Brown (219A). Claws: pale Natal Brown (219A). Pads of feet: pale Natal Brown (219A) with a grayish tinge.

DISCUSSION

This description of an adult male Poouli resembles the previous description of an adult male taken from field observations (Engilis et al. 1996), but is more detailed. The description by Engilis and coworkers (1996) has a few notable differences from my description: they report nape as "crown behind mask gray, merging on the nape to dark brown", and belly as white, but I found the nape on the adult male I caught to be Grayish Horn Color (91), and the belly a dirty Grayish Horn Color (91). They also describe the pale auricular area as a patch, whereas I found that it seems to extend in a collar almost all the way round the back of the neck, turning into a very pale gray at the back of the neck. They describe the bill as glossy black, and legs as dark pink-brown, whereas the male I captured had a Blackish Neutral Gray (82) bill, distinct from black, and Warm Sepia (221A) colored legs.

Having examined both an adult male, and an immature male (holotype) in the hand I have determined that there are a number of differences between the plumage of the adult male and that of the immature male. The crown of the immature is dark Olive-Brown (28), rather than pale gray, while its mask is dull rather than glossy, and is a dark, rich Sepia (119), with brownish tips to some feathers, rather than Jet Black (89) as on the adult male. The mask on the immature is not very extensive, and in fact above the eye only the supercilium is dark colored and part of the mask, whereas the mask is very extensive on the adult male, extending a long way behind the eye as well as a long way above and below the eye. The back of the immature is a darker shade of brown, the nape is a rich Olive-Brown (28), not Grayish Horn Color (91), while underparts are pale Tawny Olive (223D), not grayish white.

Engilis and coworkers (1996), stated that the plumage of the immature male resembles that of the adult female. From my examination of the immature male and descriptions of the adult female (Engilis et al. 1996, Pratt et al. 1997), there appear to be two key differences which may help to discriminate between adult females and immature birds in the field. Adult females are grayish on the crown with medium gray underparts, whereas the crown of the immature male is dark Olive-Brown (28), with pale Tawny Olive (223D) underparts. Differences in crown color may be the more reliable feature to separate the two age groups (pers. obs.), because color seems to be an age related difference, whereas underpart color is more likely to be variable within and between age/sex groups (pers. obs.; T. Pratt, pers. comm.).

Although the adult male I captured differed from the immature Poouli holotype in plumage it was almost identical in morphometrics to the paratype, except for exposed culmen length (adult = 15.32 mm, paratype = 14.5 mm). The mass of the paratype is unknown, but the holotype had a mass of 25.5 g (Engilis et al. 1997) and the adult a mass of 26.2 g. Although it had less mass the holotype was slightly larger in morphometrics than the adult male and paratype.

My description of an adult male also suggests that the adult male may be distinguished from the adult female in the field by crown color which is Glaucous (79)–Light Neutral Gray (85) over the whole crown for males,

and is a grayish band on the front of the crown merging into Olive-Brown (28) towards the rear of the crown for females. Adult male Poouli can also be distinguished by their Cinnamon (39) leg feathering (gray on the female) and Cinnamon (39) undertail coverts, which are buff-gray on females (Engilis et al. 1996, pers. obs.). The underpart colors and sizes of mask referred to by Pratt and coworkers (1997) may also be useful indicators of sex.

There are no descriptions of the plumage of immature females (Pratt et al. 1997), but it is probably very similar to the plumage of the immature male as in many other honeycreeper species (pers. obs.). The holotype specimen was determined to be a male by Engilis and coworkers (1996), but the paratype could not be sexed. Overall size may help to indicate sex of birds in the field because the only adult female seen during this study was noticeably smaller than the adult male that was seen feeding it.

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PAIRING CHRONOLOGY AND AGONISTIC BEHAVIORS OF WINTERING GREEN-WINGED TEAL AND MALLARDS

WILLIAM P. JOHNSON[1,2,3] AND FRANK C. ROHWER[1]

ABSTRACT.—We examined pairing chronology and aggressive interactions of Green-winged Teal (*Anas crecca*) and Mallards (*A. platyrhynchos*) wintering in coastal Louisiana from October 1994 through March 1995. Many Mallards were apparently paired upon their arrival to coastal Louisiana in early November, as 11 of the first 20 females observed were paired. Most (≥90%) female Mallards were paired by mid-December. Green-winged Teal were first observed pairing in January and 81% of females observed during March were paired. For both Green-winged Teal ($P < 0.01$) and Mallards ($P < 0.01$) intraspecific aggressive conflicts were primarily won by individuals initiating encounters. Paired Green-winged Teal ($P < 0.05$) and paired Mallards ($P < 0.05$) typically won conflicts with unpaired conspecifics. In agonistic encounters between unpaired male and unpaired female Green-winged Teal, neither sex was dominant ($P > 0.05$). The frequency of aggressive interactions by paired and unpaired Green-winged Teal was similar ($P > 0.05$); in contrast, paired Mallards were less likely to participate in aggressive interactions than were unpaired Mallards ($P < 0.01$). Effects of pairing on aggressive interactions do not appear to be the same for Green-winged Teal and Mallards. *Received 5 Dec. 1997, accepted 21 April 1998.*

Waterfowl (Anatidae) are unique among migratory birds in forming pair-bonds on wintering areas and during migration (Rohwer and Anderson 1988). Female waterfowl likely benefit from winter pair-bonds because pairs dominate unpaired conspecifics and have improved access to food resources, and because males protect their paired females from harassment (Ashcroft 1976, Jorde et al. 1983, Paulus 1983). Conversely, the demands of female attendance and defense may elevate risks of injury, decrease foraging time, and increase energetic expenditures of males when they pair (Afton and Sayler 1982, Wishart 1983). Timing of pair formation, therefore, likely represents the compromise of female benefits and male costs, both of which probably vary among species and with habitats (Hepp and Hair 1983, Rohwer and Anderson 1988).

We examined the pairing behavior of Green-winged Teal (*Anas crecca*) and Mallards (*A. platyrhynchos*) wintering in coastal Louisiana, and collected information on their agonistic activities. Surprisingly few data exist concerning these subjects for wild Mallards in the Nearctic (e.g., Heitmeyer 1985, 1988).

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METHODS

Study area.—Observations were made from October 1994 through March 1995 on the Atchafalaya River delta (29° 26′ N, 91° 20′ W), Saint Mary Parish, Louisiana. The Atchafalaya River delta is located in the eastern region of the Atchafalaya Bay and is a growing complex of shallow wetlands, mudflats, and low elevation islands (Johnson et al. 1985). Mudflats and islands are formed by natural accretion and by the pumping of dredge spoil. Daily tidal amplitude averages about 0.4 m, but it is a freshwater system. Surveys of waterfowl wintering on the delta are conducted 2–5 times a winter by Louisiana Dept. of Wildlife and Fisheries personnel. Peak survey estimates for winters 1988–1994 suggest 50,200 ± 10,600 (mean ± SE) ducks winter on the Atchafalaya River delta, the most common being Gadwall (*Anas strepera*), Green-winged Teal, and Mallards (M. R. Carloss, pers. comm.).

Observations.—We observed ducks from six elevated blinds located on mudflats adjacent to randomly chosen islands. We visited one or two blinds per day. To evenly distribute observations among mudflats we visited all six blinds in a rotation before we started another rotation. Order of visitation in each rotation was randomized. Most observations took place when tidal waters covered mudflats, because ducks were seldom near observation blinds when mudflats were exposed at low tide. Fog, particularly in late winter, limited observation hours.

We used focal individual sampling (Altmann 1974). We observed an individual bird for 5.5 min or until we lost it from view. We watched no more than one focal bird out of an individual flock during any 30 min period of the day. When Green-winged Teal and Mallards both occurred in a flock, we randomly determined which species to observe. Sex of focal individuals was randomly determined prior to observations.

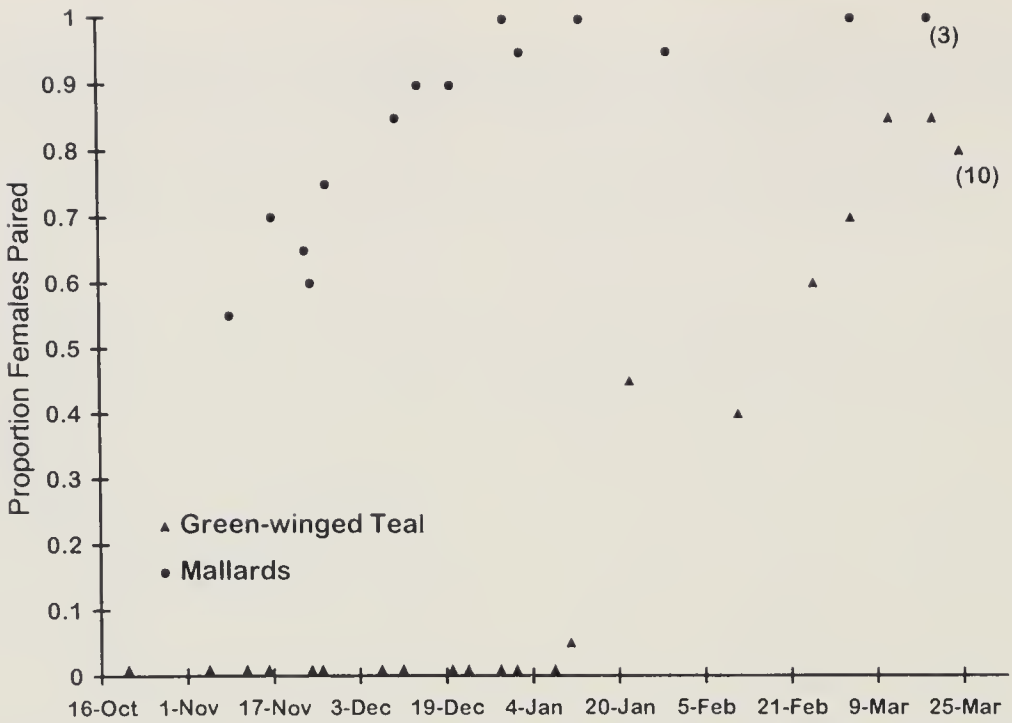

FIG. 1. Proportion of female Green-winged Teal and Mallards paired in coastal Louisiana. Each point represents 20 females unless indicated otherwise by a number in parenthesis. Sample sizes are 410 for Green-winged Teal and 263 for Mallards.

We chose focal individuals by scanning across a flock of birds, letting the spotting scope come to rest, then selecting the bird of predetermined sex and species closest to the center of the field of view (Lovvorn 1990). We recorded the pair status and aggressive interactions of focal birds. After an aggressive interaction we recorded species, sex, and pair status of the interacting bird.

The primary criterion used to determine pair status of focal individuals was sustained proximity to an individual of the opposite sex (Hepp and Hair 1983). Additionally, we used active association, such as coordination of activities or a male following a female, as indicators of pair status (Paulus 1983, Hepp and Hair 1983). By noting such criteria for a focal individual throughout the observation period, chance associations between unpaired male and female ducks were likely minimized (Weller 1965, Paulus 1983). Sex ratios of most waterfowl are male-biased (Bellrose et al. 1961, Johnson and Sargeant 1977), so we only considered females that were focal individuals when determining pairing chronology. Pair status of ducks that had aggressive interactions with focal individuals were not used in our analyses of pairing chronology because we could not observe these individuals over an extended time period to confirm their pair status.

Activities considered to be agonistic behaviors include: (1) fighting—interactions involving physical contact; (2) chasing—one bird rushing at another with no physical contact occurring; and (3) bill threats—open-beak display in the direction of another bird (Paulus 1983, Hepp and Hair 1984). Supplanting, a low-level conflict that occurs when a bird moves away from an advancing individual without a confrontation (Patterson 1982), was observed during focal sampling, but not recorded or analyzed. Supplanting is difficult to detect consistently because it involves subjective interpretation of bird movements (see also Paulus 1983).

We used χ^2 tests (Freund and Wilson 1993) to analyze frequency data concerning agonistic behaviors, and limited these data to observations lasting at least 2 min. Statistical calculations were performed on an IBM compatible personal computer using SAS (PROC FREQ, SAS Institute Inc. 1990). When investigating whether males or females were differentially involved in aggressive interactions we adjusted for skews in population sex ratio. To correct the expected frequencies we multiplied the observed numbers by the sex ratio of the local population (Hepp and Hair 1984). We obtained sex ratio data by counting males and females in a flock before focal observations began and then averaging the sex ratio per flock for the period of interest. Sex ratio information was recorded only for Mallards.

RESULTS

Pairing chronology.—Large numbers of Green-winged Teal arrived on the study area in early October, but courtship and pairing activities were not observed until late December. Paired female Green-winged Teal were first observed during the second week of January (Fig. 1), and the fraction of teal that were paired increased steadily during late winter. During March, the last month in which observations were made, 81% of females (n =

TABLE 1. Distribution of intraspecific agonistic encounters among Mallards[a] at the Atchafalaya River delta, Louisiana.

	Observed frequencies	Expected frequencies[b]	χ^2
Male	76	52.9	10.05
Female	22	45.1	11.82
Total	98	98	21.87[c]

[a] Paired and unpaired.
[b] Based on male : female ratio of 54:46. Calculations of expected frequencies follow Hepp and Hair (1984): (total number of observations) × (percentage of sex in population).
[c] df = 1, $P < 0.05$.

TABLE 2. Distribution of intra- and intersexual agonistic behaviors by Mallards at the Atchafalaya River delta, Louisiana.

Aggressor → interaction bird	Observed frequencies	Expected frequencies[a]	χ^2
Male → Male	32	20.5	6.42
Male → Female	6	17.5	7.54
Total male initiated conflicts	38	38	13.96[b]
Female → Female	5	5.9	0.15
Female → Male	6	5.1	0.17
Total female initiated conflicts	11	11	0.32[c]

[a] Based on a male : female ratio of 54:46. Calculations of expected frequencies follow Hepp and Hair (1984): (total number of observations) × (percentage of second sex in population).
[b] df = 1, $P < 0.05$.
[c] df = 1, $P > 0.05$.

62) were paired. Few Green-winged Teal remained on the study area in late March.

We observed few Mallards on the study site before 2 Nov. 1994, and we collected no data on Mallards before this date. Many Mallards apparently were paired when they arrived on the study area, as 55% of females (n = 20) observed before 9 Nov. 1994 were paired. The percent of paired females increased rapidly and stabilized near 95% during late December (Fig. 1). By March, most Mallards had left the study area.

Sex ratios. — The average sex ratio (males: females ± SE) of Mallard flocks (n = 488 flocks) during the study period was 1.17:1 ± 0.83. Sex ratios in November were 1.27:1 ± 1.90 (n = 174); in December were 1.27:1 ± 1.16 (n = 176); in January were 1.04:1 ± 0.96 (n = 93); in February were 1.08:1 ± 1.58 (n = 32); and in March were 1.00:1 ± 0.00 (n = 13). Flock size of Mallards was small, averaging 3.0 ± 0.12 (SE) birds per flock. Fifty-eight percent of flocks containing Mallards had only one pair; flocks of six or fewer Mallards typically (77%) contained an even number of males and females.

Agonistic behaviors.—Green-winged Teal (n = 792) were observed for 69.4 h. Intraspecific aggressive interactions with clear outcomes (84 of 85) overwhelmingly were won (99%) by the Green-winged Teal initiating the encounter (χ^2 = 72.4, df 1, $P < 0.01$). Among unpaired Green-winged Teal, neither males (n = 11) nor females (n = 19) were more likely to win intersexual encounters (χ^2 = 2.13, df 1, $P > 0.05$). Paired Green-winged Teal won 83% (n = 12) of their aggressive interactions with unpaired teal (χ^2 = 5.33, df = 1, $P < 0.05$). One unpaired male drove away two pairs and was responsible for both conflicts won by unpaired birds. Pair status did not influence a Green-winged Teal's likelihood of being involved in a conflict; the frequencies of aggressive interactions among unpaired (63 of 638 individuals observed) and paired (8 of 154 individuals observed) focal birds were not different (χ^2 = 2.86, df 1, $P > 0.05$).

Focal Mallards (n = 523) were observed for 46.6 h. Considering unpaired and paired Mallards together, males were more likely to engage in agonistic behaviors than were females (Table 1). For males, agonistic encounters were skewed significantly toward interactions with other males, but females were likely to interact with either males or other females (Table 2). Intraspecific aggressive interactions with clear outcomes (43 of 49) were typically won (88%) by the bird initiating the encounter (χ^2 = 42.3, df 1, $P < 0.01$). We observed only seven interactions between male and female Mallards of the same pair status, so we did not test to see if one sex was dominant. Paired Mallards were dominant to unpaired Mallards, winning 79% (n = 14) of the aggressive interactions that occurred between them (χ^2 = 4.57, df 1, $P < 0.05$). Pair status influenced a Mallard's likelihood of being involved in a conflict; the frequency of aggressive interactions among unpaired (20 of 121 individuals observed) and paired (11 of 402 individuals observed) focal birds differed (χ^2 = 26.4, df 1, $P < 0.01$). Unpaired focal male Mallards were more likely (16 of 77 individuals ob-

served) than paired focal males (5 of 185 individuals observed) to participate in agonistic activities ($\chi^2 = 19.3$, df 1, $P < 0.01$). However, unpaired focal Mallard females did not participate in more agonistic interactions (4 of 44 individuals observed) than paired focal females (6 of 217 individuals observed; $\chi^2 = 3.54$, df 1, $P > 0.05$).

Green-winged Teal did not initiate any interspecific aggressive interactions. They lost conflicts with Gadwall ($n = 2$), Blue-winged Teal (*Anas discors*; $n = 1$), Northern Pintail (*A. acuta*; $n = 1$), and Northern Shoveler (*A. clypeata*; $n = 1$). Mallards were involved in seven interspecific aggressive interactions. Mallards won conflicts with Gadwall ($n = 1$) and American Coots (*Fulica americana*; $n = 2$), but lost one conflict with a Canvasback (*Aythya valisineria*) and two of three conflicts with Mottled Ducks (*Anas fulvigula*).

DISCUSSION

Female Mallards wintering in coastal Louisiana may pair earlier and in higher proportions than Mallards wintering in Missouri (Heitmeyer 1988). In Missouri, approximately 57% of female Mallards were paired during November and 85% were paired during March (Heitmeyer 1988). In contrast, 65% of females were paired during November and 95% or more were paired from January onward in our study.

Mallards wintering in Missouri and coastal Louisiana may pair at different times because of differences in habitat. Milder conditions in Louisiana may allow Mallards to devote energy to courtship and pair maintenance earlier in the season (Afton and Sayler 1982, Baldassarre and Bolen 1986). This suggestion is made cautiously, because many of the first arriving Mallards on our study site appeared to be paired. Furthermore, the small average flock size we observed may reflect spatial separation of paired Mallards from larger flocks of unpaired birds, which were rare on our study area. During winter, paired ducks tend to use different habitats than unpaired ducks (Paulus 1983, Heitmeyer 1985), and pairs frequently occur in small groups that are segregated from unpaired ducks (Heitmeyer 1985, Paulus 1988). Spatial separation of pairs from large flocks may minimize the risks of splitting pair-bonds and the concomitant loss of time and energy spent pairing (Paulus 1988). Thus, the early pairing rates we observed for Mallards might not reflect an actual difference in timing of pair formation per se, but rather a difference in the distribution of paired versus unpaired Mallards in our region or throughout their winter range.

Pairing chronology of Green-winged Teal in the Atchafalaya River delta is quite similar to that of teal wintering in coastal North Carolina (Hepp and Hair 1983). Surprisingly, Rave and Baldassarre (1989) found later pairing dates for Green-winged Teal in coastal southwest Louisiana, where only 7% of females were paired during January and only 59% were paired during March. The similarity of pairing times for Green-winged Teal in North Carolina (Hepp and Hair 1983) and in this study confounds any attempt to explain timing differences among studies based on location or habitat type.

Although differences in pairing times among studies, for both Green-winged Teal and Mallards, might represent temporal effects, we do not believe they reflect differences in assigning pairing chronology. The studies that we cited concerning pairing chronology (i.e., Hepp and Hair 1983, Heitmeyer 1988, Rave and Baldassarre 1989, this study) used similar criteria to assign pair status.

Paired ducks are dominant to unpaired conspecifics (Jorde et al. 1983, Hepp and Hair 1984). Earlier literature (e.g., Jorde et al. 1983, Paulus 1983, Hepp and Hair 1984, Heitmeyer 1985) also suggests that unpaired male dabbling ducks dominate unpaired females. Our data on Green-winged Teal do not support this generalization; females won 63% of their encounters with males. Other cases where males do not dominate females include Mottled Ducks in Louisiana (Paulus 1988) and Blue-winged Teal, Northern Pintails, and Northern Shovelers wintering in southern Mexico (Thompson and Baldassarre 1992). Even if males are not dominant, there should be benefits to females for establishing pairs. Males are vigilant and provide their mates with protection from conspecific harassment (Ashcroft 1976, Rohwer and Anderson 1988).

Dominance of pairs, which is well established (Jorde et al. 1983; Paulus 1983, 1988; Hepp and Hair 1984; Heitmeyer 1985), may reflect early pairing of dominant individuals or may be a result of the pair-bond (Patterson

1982, Wishart 1983, Hepp 1989, Sorenson and Derrickson 1994). Green-winged Teal and Mallard pairs dominated unpaired birds and participated in fewer aggressive interactions than unpaired birds, although the second effect was not significant in Green-winged Teal.

Future studies that focus on the costs and benefits of pairing for males and females would aid our understanding of the relationships between pairing chronology, aggression, and habitats. Further research also is needed on the distribution of paired and unpaired Mallards during early winter. Information gained through such an effort might change the way degradation or loss of wetlands are viewed in areas now considered to be of secondary importance to Mallards.

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CHANGES IN SHOREBIRD AND EIDER ABUNDANCE IN THE RASMUSSEN LOWLANDS, NWT

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ABSTRACT.—Historical records of population numbers are almost entirely lacking for shorebirds and some species of waterfowl breeding in the Nearctic. In 1975 and 1976, ground surveys of breeding birds were undertaken in the Rasmussen Lowlands, Northwest Territories. We carried out similar censuses in the same area during the summers of 1994 and 1995. Weather conditions and methods were very similar during the two sets of surveys. For all years, we compared densities in different habitat types, as well as estimates for the entire region of total numbers of breeding Red Phalaropes (*Phalaropus fulicaria*), Pectoral Sandpipers, (*Calidris melanotos*), White-rumped Sandpipers (*C. fuscicollis*), Semipalmated Sandpipers (*C. pusilla*), Black-bellied Plovers (*Pluvialis squatarola*), American Golden-Plovers (*Pluvialis dominica*), Dunlin (*C. alpina*), Baird's Sandpipers (*C. bairdii*), and King Eiders (*Somateria spectabilis*). We found that breeding populations of Red Phalaropes, Black-bellied Plovers, American Golden-Plovers, and King Eiders in the 1990s had decreased substantially (76–87%) from their numbers in the 1970s. Numbers of other shorebird species did not decrease significantly (17–48%). Numbers of Black-bellied Plovers have apparently decreased at staging sites on the east coast of the United States and Canada. However, for American Golden-Plovers, there is no evidence of a decline on the east coast or in at least one other area in the eastern Nearctic. No other population information exists for Red Phalaropes breeding in the eastern Nearctic. Eider numbers appear to be decreasing throughout the Arctic. Possible reasons for declines are habitat changes in migratory staging sites and southern wintering areas. We need more consistent monitoring of arctic shorebirds in order to identify species with continual population declines. Further studies should emphasize Nearctic populations of species showing substantial declines in this study, examining consistency of decreases throughout the Nearctic, and reasons for such changes. *Received 9 Oct. 1997, accepted 15 May 1998.*

Very little historical information exists on population numbers of shorebirds breeding in the Nearctic. Since few species of shorebirds breeding in the northern hemisphere are considered in immediate danger of extinction, this might not appear to be cause for concern. However, several factors about the biology of these birds make them particularly vulnerable. Many species gather in very large numbers at specific and consistent staging sites each year, acquiring enough energy to fly to their next foraging site (Senner and Howe 1984). For example, flocks of more than 200,000 Semipalmated Sandpipers (*Calidris pusilla*) can be found in the Bay of Fundy during fall migration in July (Morrison and Harrington 1979, Hicklin 1987). Therefore, at any of these major migratory staging areas, a large portion of one or more populations are extremely vulnerable not only to some catastrophic event when the birds are present (such as an oil spill), but also to any permanent habitat changes at that staging site. A decline in food abundance, or even changes in timing of peak food availability, might result in birds being unable to successfully continue their flight. This would be particularly important in areas such as the Bay of Fundy where the birds must migrate large distances nonstop over oceans. Total loss of an important staging site to development, pollution, or even drought, could have very severe consequences to populations of these birds (Myers 1983, Morrison 1984, Senner and Howe 1984, Myers et al. 1987). Most shorebirds are highly dependent on wetland environments, both coastal and inland. Such habitats are among the most heavily affected by human activity. A considerable percentage of North and South American wetlands are at risk or have already been lost or degraded by industry, recreation, or agriculture (Dahl 1990, Gillispie et al. 1991, Canevari et al. 1998).

In terms of population stability, even small changes in survivorship of adult shorebirds

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apparently have greater consequences than variations in breeding productivity (Hitchcock and Gratto-Trevor 1997). These birds are fairly long-lived and have the potential to produce only a few young each year. Clutches typically consist of no more than four eggs, and in the Arctic, renesting after clutch loss is not common. For most shorebirds, no more than one brood is produced per year, and fledging success can be low (Evans and Pienkowski 1984). Therefore, conditions during migration and wintering are very important, and recovery after a major population decline could potentially be slow. Even species with large populations can crash and disappear very rapidly, as with the Eskimo Curlew (*Numenius borealis*) earlier this century (Gollop et al. 1986).

Most species of North American shorebirds breed almost entirely in the Arctic (Godfrey 1986), so we cannot use the Breeding Bird Surveys of the United States and southern Canada to monitor changes in their population numbers. A few studies have used trend analysis to look at population changes in shorebirds staging in eastern North America during migration (Howe et al. 1989, Morrison et al. 1994), and a very few studies have examined long-term population changes on the breeding grounds, usually in a small study area (e.g., Pattie 1990, Gratto-Trevor 1994, Hitchcock and Gratto-Trevor 1997). In this paper we describe a unique opportunity to examine long-term changes in numbers of shorebirds across a fairly large (7500 km^2) area of the Canadian Arctic.

In 1975 and 1976, ground surveys for shorebirds and other birds were carried out in the Rasmussen Lowlands, Northwest Territories, by McLaren and coworkers (1977). These studies were instigated because the area was on the route of the proposed Polar Gas Pipeline. The surveys demonstrated that the Rasmussen Lowlands supported a high diversity and density of breeding birds, particularly shorebirds. In 1994 and 1995, almost 20 years later, we were able to re-census the area and consider changes in the bird population between the mid 1970s and the mid 1990s. The purpose of this paper is to report changes in abundance of shorebirds and eiders between the 1970s and 1990s in the Rasmussen Lowlands, NWT, to determine if similar trends in population changes exist in other studies and areas for these species, and to discuss possible reasons for any major population changes. Eiders are included because there recently has been considerable concern expressed about their numbers throughout the Arctic (Dickson 1996, Turner et al. 1996).

STUDY AREA AND METHODS

Study area.—The Rasmussen Lowlands are situated in the central Canadian Arctic on the mainland coast, at the eastern side of the Rasmussen Basin (Fig. 1). The nearest settlement is Taloyoak, about 55 km north of the northern edge of the study area. In this isolated region, no major land use changes have occurred since the 1970s. Much of the area is flat and poorly drained with some eskers and rock outcrops. Numerous lakes and ponds are present, and tussocky tundra and sedge marshes are common. The most common shorebirds breeding in the area (in order of abundance in the 1990s) are Red Phalaropes (*Phalaropus fulicaria*), Pectoral Sandpipers, (*Calidris melanotos*), White-rumped Sandpipers (*C. fuscicollis*), Semipalmated Sandpipers (*C. pusilla*), Dunlin (*C. alpina*), American Golden-Plovers (*Pluvialis dominica*), Black-bellied Plovers (*Pluvialis squatarola*), and Baird's Sandpipers (*C. bairdii*). King Eiders (*Somateria spectabilis*) are also common breeders in the area.

Red Phalaropes are highly aquatic birds that breed in the mid to high Arctic, and winter in southern oceans (Cramp and Simmons 1983). Pectoral (Godfrey 1986, Parmalee 1992) and White-rumped (Godfrey 1986, Marchant et al. 1986) sandpipers are small polygynous shorebirds that winter primarily in mid to southern South America. Semipalmated Sandpipers, Dunlin, and Baird's sandpipers are small monogamous sandpipers. Semipalmated Sandpipers winter mainly in northern South America (Gratto-Trevor 1992), Dunlin along coasts of the United States and southern Canada (Warnock and Gill 1996), and Baird's Sandpipers primarily in the southern half of South America (Myers and Myers 1979). Black-bellied Plovers and American Golden-Plovers are both large monogamous plovers. Black-bellied Plovers winter in coastal areas from the United States to southern South America (Paulson 1995), while American Golden-Plovers migrate to the grasslands of central South America (Johnson and Connors 1996). Since King Eiders breed, stage, and winter in the north, there is less information about their population numbers than about many other species of waterfowl (Bellrose 1976, Godfrey 1986, Dickson 1996).

Methods.—Methods were similar during the 1970s and 1990s studies and should not have resulted in significant differences in population estimation. Overall, 20% of all 1990s plots were in the same location as 1970s transects. Plot locations in 1994 were chosen to provide a mixture of plots in the same location as 1970s transects as well as plots in various habitat types (as represented by different colors on the initial satel-

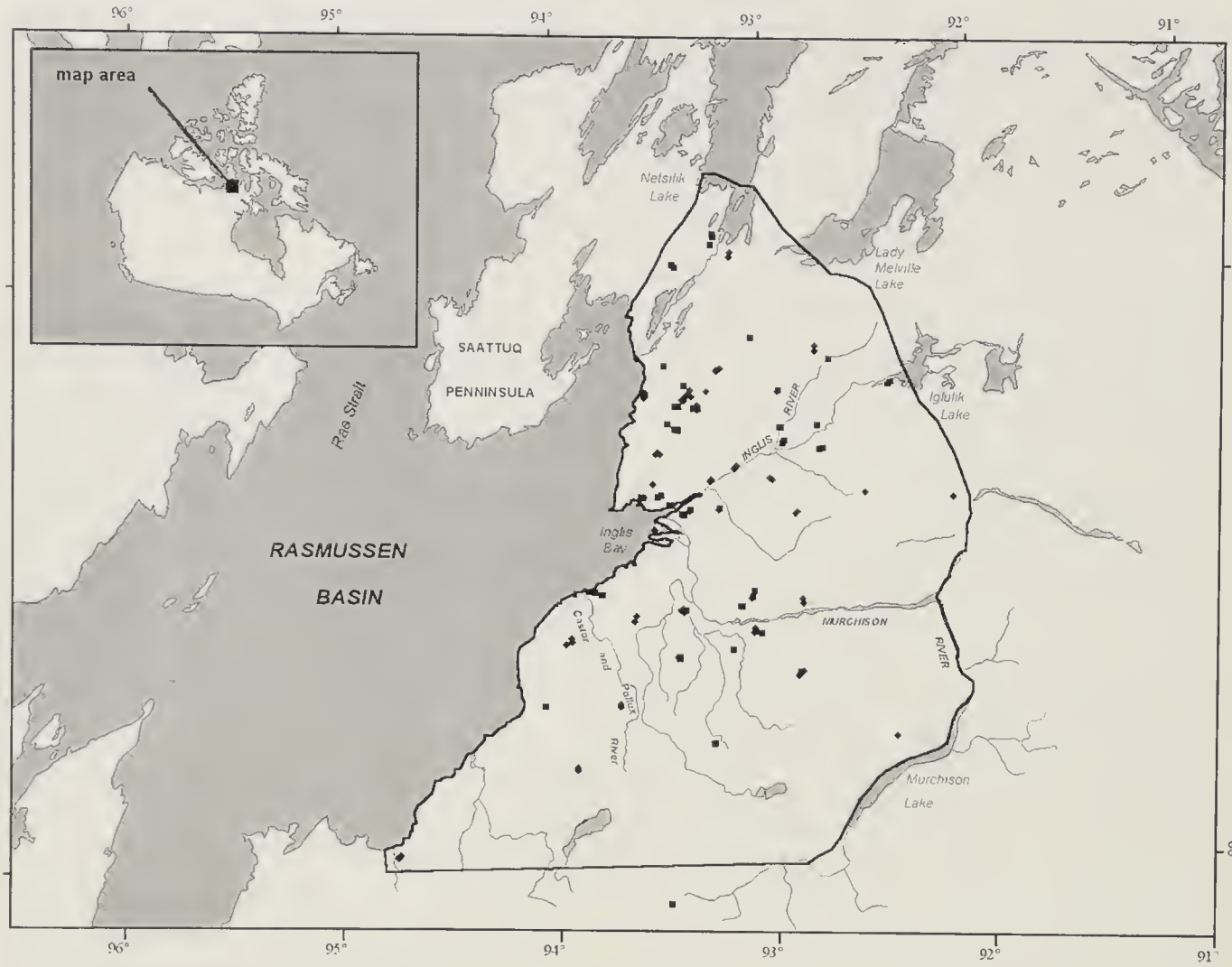

FIG. 1. Rasmussen Lowlands, NWT, study area.

lite imagery) spread throughout the study area (Fig. 1). Eleven 1994 plots were re-censused in 1995. Otherwise, plot locations in 1995 were selected to fill in geographic areas and habitats less well sampled the previous year. In both 1994 and 1995 we deliberately over-sampled sites with expected 'good' shorebird habitat, as identified by satellite imagery.

Censuses in the McLaren's and coworkers' (1977) study were transects 56 m wide and 933–9719 m long (for a total area of 14 km^2 over both years). Two people walked 28 m apart, so they would have been no farther than 14 m from any incubating bird. We used 400 × 400 m plots (a total of 21 km^2 over both years) censused by transects of 2 people walking 25 m apart. All parts of each plot were censused in this way, so we could have been no farther than 12.5 m from any incubating bird. Habitats and behavior of all birds, and their locations within and outside transects were noted in both studies. McLaren and coworkers (1977) described habitat variables at the start of the transect and every 130 m or when the habitat changed noticeably. We documented habitat variables at the start of the plot, every time the habitat changed noticeably, and drew maps of the extent of different habitats within each plot. On these field maps we also marked the location of each bird observed.

To make habitat types comparable for both studies, habitats were lumped into the following six categories: dwarf shrub tundra, with dwarf shrub and moss dominant, moist to dry soil, more than 50% cover [includes McLaren et al. (1977) dwarf shrub tundra open and closed phases]; graminoid/dwarf shrub tundra, with graminoids and dwarf shrub co-dominant, dry to moist soil, greater than 50% cover [McLaren et al. (1977) graminoid-dwarf shrub tundra open and closed phases]; low tundra, with graminoids, especially *Carex*, and moss dominant, soil saturated or with standing water, greater than 50% cover [McLaren et al. (1977) dry and wet *Carex* tundra open and closed phases, plus graminoid-lichen tundra closed phase]; moss tundra, with moss and lichen dominant, more than 80% plant cover, soil moisture dry to moist [McLaren et al. (1977) lichen-moss tundra closed phase]; sparse tundra, variable plant types and soil moisture but less than 50% plant cover, characterized primarily by a lack of vegetation [McLaren et al. (1977) sparse phases of lichen-moss tundra, graminoid-dwarf shrub tundra and dwarf shrub tundra]; and tussocky tundra, with cottongrass (*Eriophorum*) as the dominant plant, graminoids and moss dominant, and saturated soil to standing water, greater than 50% cover [McLaren et al. (1977) dry and wet cottongrass tundra closed phase]. Unvegetated

ground was excluded from analyses, as virtually no birds were found there in either study.

Overall timing of the censuses was similar in both studies (1970s: 20 June to 17 July vs 1990s: 18 June to 13 July), encompassing much of the incubation and early brood-rearing periods of all birds present. Arctic weather can have extreme effects on the number of birds breeding in a year (Evans and Pienkowski 1984, Gratto-Trevor 1991). Weather conditions were also comparable between the studies, with each having apparently one year with warmer than usual summer weather (and early snow melt), and one year with colder than normal summer temperatures (and later snow melt; Johnston, Gratto-Trevor and Pepper, unpubl. data).

Only birds seen within the transect or plot areas were included in data analyses. Birds outside the area or flying overhead were noted but excluded from further analysis in both studies. Both excluded flocks of five or more birds. In both studies, large ponds and lakes were excluded from calculations of area searched. McLaren and coworkers (1977) calculated bird densities as the total number of birds of a species seen during censuses divided by the total land area searched (of that habitat, or total area) each year. We used weighted means of birds per area of habitat in each plot, and were therefore able to calculate 95% confidence limits around our mean densities. We back-checked and determined that these mean densities per habitat type each year for each species were virtually identical to densities obtained by dividing total birds seen during censuses by total area searched (of that habitat or total area) each year: McLaren's and coworkers' (1977) methods.

McLaren and coworkers (1977) sampled habitats in the same proportion that they existed in the study area. We used a stratified random design, where we concentrated on certain habitat types (those expected to contain the most birds) more than others. Since McLaren and coworkers (1977) felt that their transects represented an unbiased choice from the available habitat, they calculated their estimates of total population size by multiplying a species' density by the total area in the region. Because we deliberately oversampled some habitat types, we calculated our total population estimates by multiplying density in habitat 1 by total regional area of habitat 1 plus density in habitat 2 × total area of habitat 2 and so on. We determined total area of each habitat type in our study via Landsat Thematic Mapper analysis (Johnston, Gratto-Trevor and Pepper, unpubl. data). Our total study area (Fig. 1) was 77% of the area used by McLaren and coworkers (1977) for their total population estimates, so their totals were multiplied by 0.77 to adjust for the difference.

RESULTS

Because the densities and population estimates reported by McLaren and coworkers (1977) have no associated variance, we could not easily compare them statistically with our results. We decided to compare our numbers in two general ways: species densities in each habitat type, and overall population estimates.

Densities per habitat type.—For each of the eight most common shorebird species, and for King Eiders, we compared McLaren's and coworkers' (1977) and our densities in each of the six habitat types (Table 1). Both years of each study were combined because McLaren and coworkers (1977) presented their results in that form. If their species densities in a habitat type were above or below our 95% confidence limits for that habitat, we considered the difference significant. Red Phalarope density decreased significantly only in the low tundra habitat. All decreases (significant or not) were in habitats that contained the most phalaropes in the 1970s. On the other hand, Pectoral, Semipalmated, Baird's and White-rumped sandpipers did not show any significant changes between the 1970s and 1990s; nor did Dunlin. There were significant decreases of Black-bellied Plovers in low tundra and tussocky tundra habitats and significant decreases of American Golden-Plovers in low tundra and moss tundra. King Eider densities significantly declined from the 1970s to 1990s only in moss tundra.

Total population estimates.—We compared overall McLaren's and coworkers' (1977) population estimates each year with our mean estimates and 95% confidence limits for each species (Fig. 2). If their number was above or below our 95% confidence limits, we considered the difference significant. Only one year (1976) of ground survey information was available for King Eiders from the 1970s.

For Black-bellied Plovers, Red Phalaropes, and King Eiders, in all possible comparisons, 1990s upper 95% confidence limits were lower than the 1970s population estimates (Fig. 2). Although the population estimates of American Golden-Plovers were very low in both 1994 and 1995, 95% confidence limits were significantly lower than 1970s estimates only in 1995. In 1994 the variance was greater. The 1970s population estimates were always contained within the 1990s confidence estimates for Dunlin and Semipalmated Sandpipers, and the same was true in three of the four possible comparisons (1994 vs 1975 and 1976, 1995 vs 1975 and 1976) for Baird's

TABLE 1. Densities of shorebirds in different habitat types in the Rasmussen lowlands, NWT: 1975–1976 versus 1994–1995.

	Birds/km^2					
Years[a]	Dwarf shrub[b] tundra	Graminoid/ dwarf shrub tundra	Low tundra	Moss tundra	Sparse tundra	Tussocky tundra
Red Phalarope						
1975/6	2	9	68	9	0	16
1994/5	3	2	12	9	3	3
Trend[c]	=	↓↓	↓↓↓	=	↑	↓↓
C.L. 1900s[d]	−3 to 8	−6 to 10	−4 to 27	−12 to 30	−8 to 13	−17 to 24
Significance[e]	—	—	*	—	—	—
Overall Trend: Decrease						
Pectoral Sandpiper						
1975/6	9	2	10	2	3	7
1994/5	5	6	6	4	2	6
Trend[c]	↓	↑	↓	↑	=	=
C.L. 1900s[d]	−5 to 15	−8 to 19	−2 to 15	−10 to 18	−3 to 6	−13 to 24
Significance[e]	—	—	—	—	—	—
Overall Trend: No Change						
White-rumped Sandpiper						
1975/6	7	6	6	7	0	2
1994/5	6	6	6	4	2	3
Trend[c]	=	=	=	↓	↑	=
C.L. 1900s[d]	−7 to 19	−13 to 24	−6 to 18	−7 to 16	−3 to 7	−27 to 34
Significance[e]	—	—	—	—	—	—
Overall Trend: No Change						
Semipalmated Sandpiper						
1975/6	1	2	4	0	6	1
1994/5	2	1	3	2	3	0
Trend[c]	=	=	=	↑	↓	=
C.L. 1900s[d]	−5 to 9	−2 to 4	−8 to 14	−5 to 10	−5 to 11	0
Significance[e]	—	—	—	—	—	—
Overall Trend: No Change						
Black-bellied Plover						
1975/6	7	2	5	0	0	5
1994/5	1	0	1	1	1	0
Trend[c]	↓↓	↓	↓↓	=	=	↓↓
C.L. 1900s[d]	−8 to 9	−1 to 2	−2 to 3	−2 to 3	−3 to 5	−1 to 2
Significance[e]	—	—	*	—	—	*
Overall Trend: Decrease						
American Golden-Plover						
1975/6	3	4	3	9	0	0
1994/5	3	2	1	1	0	0
Trend[c]	=	↓	↓	↓↓↓	=	=
C.L. 1900s[d]	−12 to 17	−2 to 5	−1 to 2	−6 to 8	0	0
Significance[e]	—	—	*	*	—	—
Overall Trend: Decrease						
Dunlin						
1975/6	0	2	0	0	0	1
1994/5	0	0	2	1	0	4
Trend[c]	=	↓	↑	=	=	↑
C.L. 1900s[d]	−2 to 3	−1 to 2	−2 to 5	−5 to 7	0	−8 to 17
Significance[e]	—	—	—	—	—	—
Overall Trend: No Change						

TABLE 1. CONTINUED

Years[a]	Birds/km^2					
	Dwarf shrub[b] tundra	Graminoid/ dwarf shrub tundra	Low tundra	Moss tundra	Sparse tundra	Tussocky tundra
Baird's Sandpiper						
	0	0	1	2	0	0
1975/6	0	1	0	1	1	0
1994/5	=	=	=	=	=	=
Trend[c]	−1 to 2	−3 to 4	−1 to 2	−3 to 4	−4 to 6	0
C.L. 1900s[d]	—	—	—	—	—	—
Significance[e]						
Overall Trend: No Change						
King Eider						
	1	3	4	4	0	2
1975/6	0	0	1	1	0	0
1994/5	=	↓	↓	↓	=	↓
Trend[c]	−1 to 2	−3 to 4	−1 to 2	−3 to 4	−4 to 6	0
C.L. 1900s[d]	—	—	—	*	—	—
Significance[e]						
Overall Trend: Decrease						

[a] Data from 1975 and 1976 are combined (from McLaren et al. 1977), as are data from 1994 and 1995.
[b] See text for description of habitats.
[c] Trend: '=' if change is 1 or 0, '↑' increase, '↓' decrease; the more arrows, the greater the change.
[d] C.L. 1990s: 95% confidence limits for 1994/5.
[e] Significance: '—' = 1970s value within 1990s 95% confidence limits; '*' = 1970s value outside 1990s 95% confidence limits.

Sandpipers, Pectoral Sandipers, and White-rumped Sandpipers (Fig. 2). Overall then, results were consistent with the previous density/habitat comparisons; in all species where there was a significant decrease in density per habitat between the 1970s and 1990s (which were also all species where more densities tended to go down than up), there were significant declines in overall numbers between the two time periods (Table 1, Fig. 2). Since overall population numbers were calculated from habitat densities, it is reassuring, but not particularly surprising, that results were consistent between overall numbers and density comparisons. Numbers of breeding Red Phalaropes, Black-bellied Plovers, American Golden-Plovers, and King Eiders (Fig. 2) apparently decreased significantly in the Rasmussen Lowlands between 1975/76 and 1994/95. Numbers of Pectoral Sandpipers, White-rumped Sandpipers, Semipalmated Sandpipers, Baird's Sandpipers, and Dunlin (Fig. 2) did not change significantly.

In the 1970s, 43% of the shorebirds seen in the area were Red Phalaropes (McLaren et al. 1977); in the 1990s this decreased to 27%. In terms of total population estimates, combining numbers from 1975 and 1976, and 1994 and 1995, the following declines were significant: Red Phalaropes decreased by 76%, Black-bellied Plovers by 87%, American Golden-Plovers by 79%, and King Eiders by 86%.

DISCUSSION

Validity of comparisons.—Methods were not identical for both time periods, and this may have resulted in differences in density and overall population estimates. If anything, this would have made our 1990s numbers higher, not lower. For example, a greater percentage of secretive birds (such as many species of nesting shorebirds) are missed in transects versus plot censuses (Edwards et al. 1981). Although the spread in timing of censuses is similar between the 1970s and the 1990s studies, a greater proportion of McLaren's and coworkers' (1977) ground surveys were carried out later in the season. This would result in relatively fewer birds being observed in the 1970s because of the early migration of failed breeders, nonbreeders, and nonincubating parents in uniparental species. Young of the year were not counted during the surveys in the 1970s or 1990s because

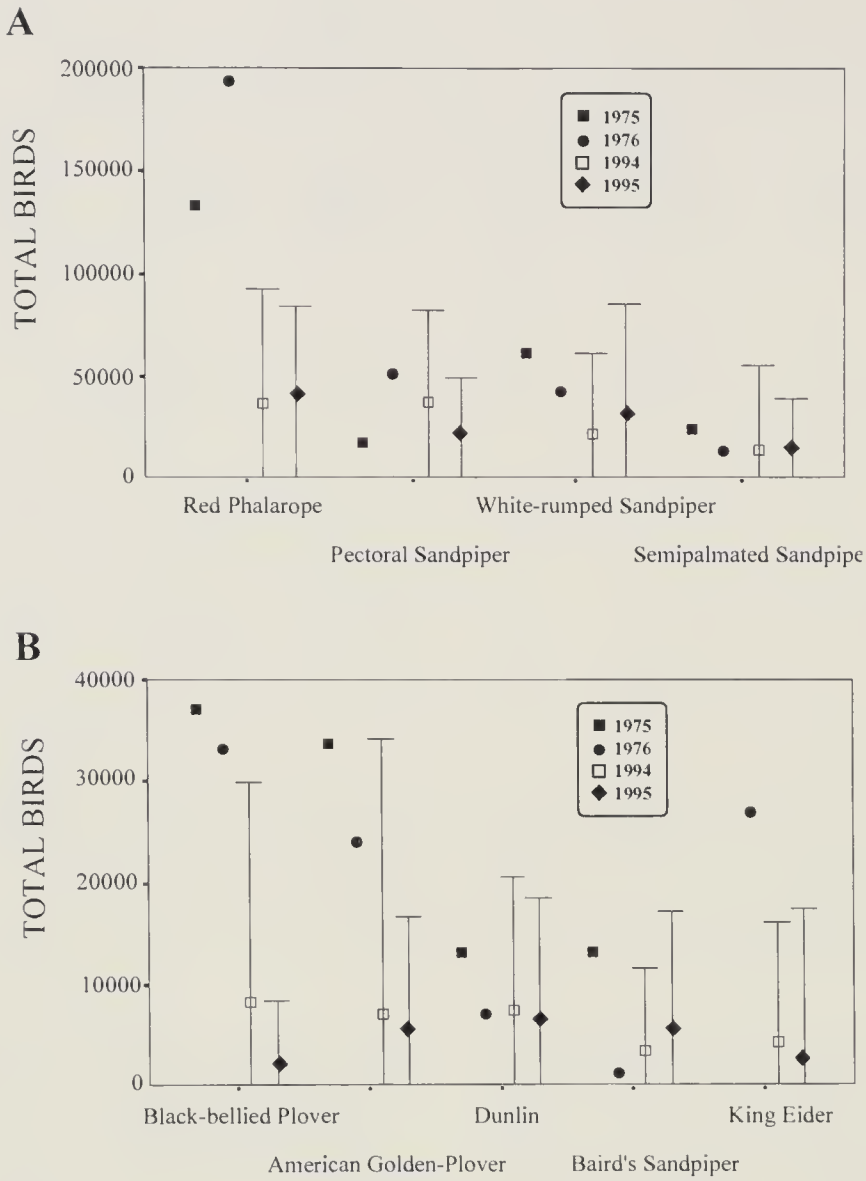

FIG. 2. Total estimated bird populations in 7500 km^2 area of Rasmussen Lowlands. Data from 1975 and 1976 were taken from McLaren and coworkers (1977). Bars around 1994 and 1995 data represent 95% confidence limits.

they were rarely seen before fledging, and very few fledged before the surveys ended. Groups of more than five birds were excluded from analysis in both studies, so few migrants were counted (Gratto-Trevor 1994, unpubl. data). Weather conditions in 1976 were apparently worse than either 1994 or 1995, again suggesting relatively lower numbers for the 1970s. There was no visual indication of habitat degradation from the 1970s to the 1990s, and no reason to expect any.

If McLaren and coworkers (1977) were incorrect in their assumption that their transects randomly surveyed the available habitat, they may have over or underestimated total population numbers. However, the habitat density results would not have been affected by such an error, and these data show significant declines in at least one habitat type for both species of large plovers, phalaropes, and eiders. This suggests that changes in numbers between the two time periods are not due to differences in methodology, and may be even greater than reported here.

Trends in other areas and possible reasons for declines.—For all of the species examined here, little information exists on changes in population numbers from other studies. However, for King Eiders, major declines have been noted in Alaska (Conant and Groves 1995), and numbers in the central and western Canadian Arctic appear to have decreased as well (Dickson et al. 1997). In the Rasmussen region itself, residents have expressed concern over decreasing eider numbers (K. McCormick, pers. comm.). Large decreases have

been noted among eiders wintering in Greenland, but it is not known what percentage of King Eiders nesting in the Rasmussen Lowlands winter in Greenland, versus Labrador and Newfoundland. One reason suggested for the decline in King Eiders is overharvesting of eiders in Greenland and possibly Newfoundland and Labrador (Turner et al. 1996). However, reasons for the decline may not be specific to King Eiders. Global factors such as changes in marine conditions on wintering grounds may be affecting prey abundance for many seabird species (Goudie et al. 1994).

For Red Phalaropes, there is no indication of a population decline of Alaskan breeding populations (Troy 1996; D. Schamel, pers. comm.). Other than the current study, apparently no information exists for the central or eastern Nearctic. Large numbers of Red Phalaropes have historically staged off Brier Island, Nova Scotia, in the fall (Squires 1952, Brown 1980), and it is not known whether their numbers there have decreased recently (C. D. Duncan, pers. comm.; P. Hicklin, pers. comm.). Wintering areas of central and eastern Nearctic breeding Red Phalaropes are unverified, and no wintering trend information exists for this species. A major southeastern autumn migration of Nearctic populations has been suggested, with the birds wintering in upwellings of the Guinea and Canary currents off the bulge of Western Africa (Cramp and Simmons 1983). Red-necked Phalaropes (*Phalaropus lobatus*) are very similar to Red Phalaropes. Both are plankton feeders and highly aquatic, so similar factors might be expected to affect these two species. The many thousands of Red-necked Phalaropes that used to stage in the Bay of Fundy (Duncan 1995), and the large numbers historically found off Japan, no longer occur there (Rubega and Schamel, in press). No one knows why these populations have disappeared, nor is it known whether the birds have moved or died. The major wintering concentrations of Nearctic Red-necked Phalaropes are apparently in the Humboldt current off Peru, South America (Cramp and Simmons 1983).

Possible reasons for declines in populations of phalaropes are changes in abundance or availability of their plankton prey in staging or wintering areas. Global conditions may be affecting upwelling sites, where plankton are forced to the surface during daytime, becoming available for foraging phalaropes (Brown 1980, Cramp and Simmons 1983).

For Black-bellied Plovers, analysis of east coast staging areas revealed decreases that approached significance in their numbers during migration (for a cumulative decline of 46% over 12 years and 33% over 10 years, respectively; Howe et al. 1989, Morrison et al. 1994). No data exist from wintering areas. Bloodworm harvesting in the Bay of Fundy significantly decreased Black-bellied Plover foraging success (Shepherd 1994). However, bloodworm harvesting began too recently in Nova Scotia to have resulted in population declines, and harvesting in the eastern United States was not concentrated in important Black-bellied Plover foraging habitat (P. Shepherd, pers. comm.).

American Golden-Plovers increased during a long-term study on Devon Island, NWT, and no changes were noted in birds staging in eastern Canada (Pattie 1990, Morrison et al. 1994). No data exist from wintering areas, although some researchers have noted that considerable portions of the winter range are at risk to agriculture, and this might result ultimately in population declines (Johnson and Connors 1996).

Other than the fact that both Black-bellied Plovers and American Golden-Plovers are large plovers that migrate south relatively late in the fall, there seems little similarity between the two species that would explain the large decreases found in their populations at the Rasmussen Lowlands. It seems unlikely that hunting in South and Central America, or illegal hunting in eastern Canada and the United States could explain the decline (Johnson and Connors 1996), but shorebird mortality by hunting is largely undocumented (Senner and Howe 1984).

Conclusions.—We observed major declines in numbers of three species of shorebirds and in King Eiders between the mid 1970s and the mid 1990s. Reasons for these decreases are unclear, and they may be different for each species. In some cases, population declines in these species were observed during other studies as well. In other instances there were no changes elsewhere, or more often, no data. It is not known how consistent these changes are throughout even the eastern Nearctic, but

the Rasmussen Lowlands are in themselves a large area, consisting of at least 7500 km^2. Since numbers were not censused between 1976 and 1994, we cannot be certain that the decreases represent a persistent and continuing decline. It is possible that they are natural fluctuations, perhaps the result of a series of recent poor breeding years. To determine whether population numbers again increase, or continue to decline, future researchers should recensus the area more frequently, perhaps every two years out of ten. More information must be obtained on population trends and factors affecting productivity and survival in this region as well as elsewhere in the Nearctic.

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SPRING MIGRATION OF SHOREBIRDS ON THE YAKUTAT FORELANDS, ALASKA

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ABSTRACT.—During spring 1996 and 1997, we conducted ground surveys at high tide to determine species composition, numbers, and timing of spring shorebird migration on the Yakutat Forelands, Alaska. Western Sandpipers (*Calidris mauri*) and Dunlins (*C. alpina*) were the most abundant shorebirds we observed in the Seal Creek-Ahrnklin River estuary; we also observed large aggregations of Marbled Godwits (*Limosa fedoa beringiae*). Using information on turnover rates of radio-tagged Western Sandpipers, we estimated that about 101,000 small calidridine sandpipers used the Seal Creek-Ahrnklin River estuary as a spring migration stopover annually in 1996 and 1997. From previous aerial survey data on shorebird distribution, we estimated that the entire Yakutat Forelands supports a spring population of more than 350,000 migrant shorebirds. Therefore, the forelands is an important stopover site to migratory shorebirds and should be included in the network of international stopover sites needed to conserve shorebirds migrating along the Pacific coast. *Received 22 Oct. 1997, accepted 30 Mar. 1998.*

Each spring, millions of shorebirds migrate north along the Pacific coast of North America to Arctic and sub-Arctic breeding grounds from temperate or tropical wintering grounds. To replenish depleted fat reserves during migration shorebirds congregate on coastal tidal flats that are often geographically restricted (Myers et al. 1987). Concentrations of shorebirds on large tidal flats can reach impressive numbers (Myers 1983). For example, most (>60%) of the world's Western Sandpipers (*Calidris mauri*), the most abundant shorebird migrant along the Pacific coast (Butler et al. 1996), stop at the Copper-Bering River Delta, Alaska, during spring migration; single-day counts in early May can exceed one million individuals (Isleib 1979, Iverson et al. 1996). Several other concentration areas along the Pacific coast annually support more than one million migratory shorebirds (e.g., Gray's Harbor, Washington; San Francisco Bay, California; Fraser River Delta, British Columbia; Page and Gill 1994, Gill et al. 1995). Protection of these primary concentration sites is critical to the conservation of migratory shorebirds and is central to the mission of the Western Hemisphere Shorebird Reserve Network (WHSRN) program (Finney 1995).

Recent evidence from the Pacific Coast (Iverson et al. 1996) and Great Plains (Skagen and Knopf 1994) suggests that small, secondary wetlands also provide important shorebird stopover habitats. Radio-tagged Western Sandpipers used short flights (generally <1000 km) to migrate between a series of coastal wetlands along the Pacific Coast, and Great Plains migrants used alternative wetlands when environmental perturbations altered the quality and availability of traditionally-used wetlands. Although most primary stopover areas have been identified, information on the importance of secondary wetlands is still needed. Evidence from aerial surveys for radio-tagged Western Sandpipers (Bishop, unpubl. data) indicated that small estuaries on the Yakutat Forelands, heretofore thought to be of minor importance to migratory shorebirds, might provide stopover habitat for shorebirds that migrate along the Pacific coast of Alaska. In fact, when Senner and coworkers (1981) assessed patterns of spring migration of Western Sandpipers in southern Alaska, little information was available about their migration between the Fraser River Delta and the Copper-Bering River Delta, Alaska. Senner (1979) earlier suggested that Western Sandpipers might use a series of stopover sites but had no quantitative information from any site in southeastern Alaska to evaluate his hypothesis. Because no intensive study of estuaries on the forelands has been conducted, we initiated a project to determine species composition, numbers, and timing of spring shorebird migration on the Yakutat Forelands and to assess its importance as a stopover habitat.

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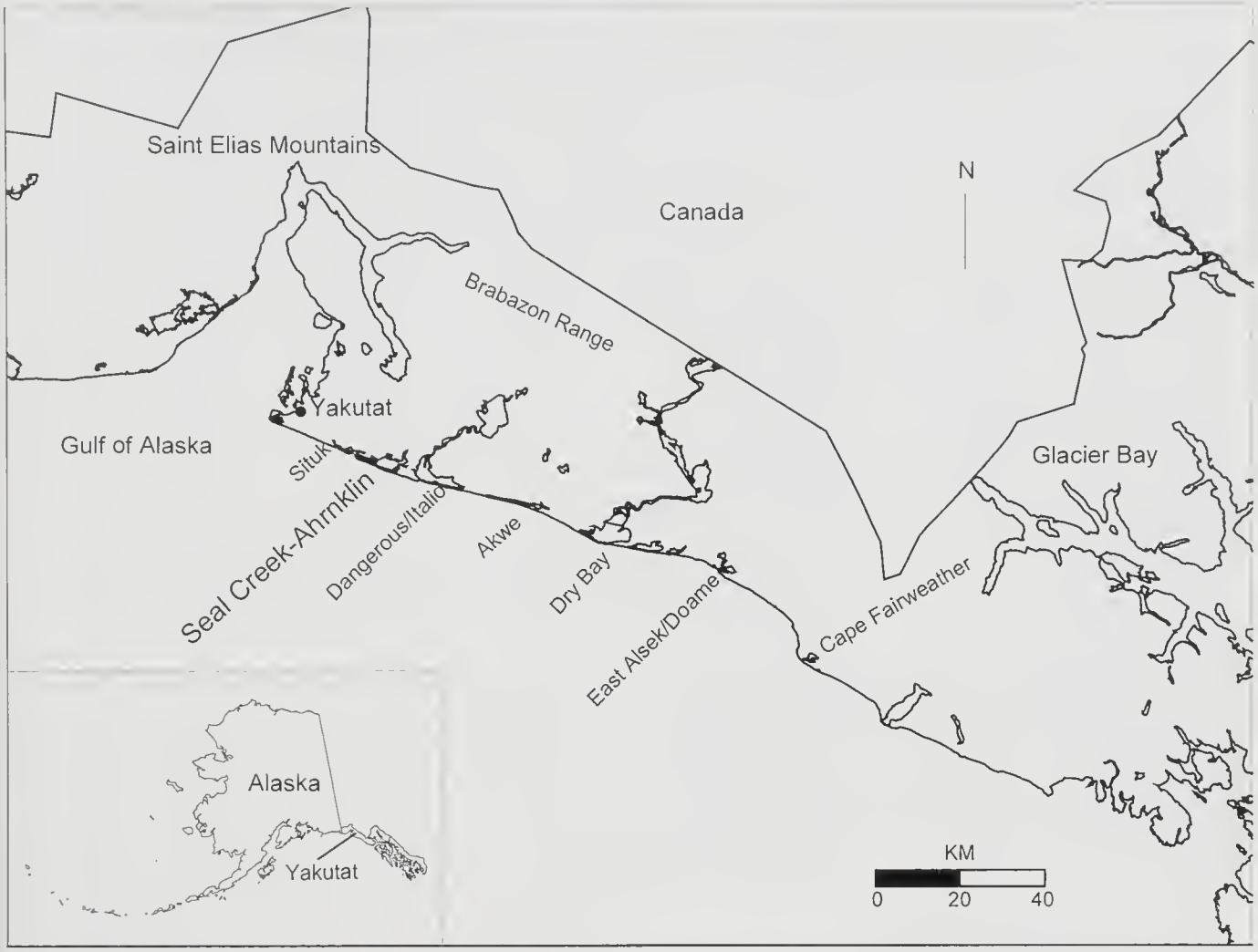

FIG. 1. Location of spring (1996, 1997) shorebird study area (Seal Creek-Ahrnklin River), other estuaries, and the village of Yakutat on the Yakutat Forelands, Alaska.

STUDY AREA AND METHODS

The Yakutat Forelands is located along the Pacific Coast of Alaska and extends 140 km from the village of Yakutat (59° 30′ N, 139° 50′ W) in the northwest to Cape Fairweather (58° 48′ N, 138° 00′ W) in the southeast (Fig. 1). This glacial plain varies in width from 30 to 70 km and is bounded on the east by the Saint Elias Mountains and Brabazon Range and on the west by the Gulf of Alaska. The forelands is characterized by sandy beaches, extensive sand dunes, tidal mudflats, deciduous shrublands, spruce forests, and muskegs, and is transected by a series of relatively short, mostly clear-running rivers (Patten 1982). Because of barrier sand-dune islands, considerable tidal flats are associated with almost all rivers that flow into the Gulf of Alaska. Aside from the Copper-Bering River Delta, the forelands provides the most extensive estuary and wetland habitat along the eastern Gulf of Alaska coast. Most of the forelands is managed by the U.S. Forest Service as part of the Tongass National Forest.

Because of numerous detections of radio-tagged Western Sandpipers made in 1995 (D. Walter, pers. comm.), we concentrated our survey effort in the Seal Creek-Ahrnklin River estuary (Fig. 1). Water depth limited our access and we had to restrict our ground surveys to about 20.5 km^2 (42%) of the estuary. In this area, we established a series of 13 points that we surveyed between two hours before and two hours after high tide; we used a motorized skiff to travel between points. Points were systematically located to cover all of the intertidal area and to minimize double-counting. At each point, two observers scanned different areas of barren or sparsely-vegetated tidal flats and identified and counted each shorebird species detected; large flocks were counted by tens. Counting areas at each point were divided between observers, and natural or flagged landmarks were used to eliminate double-counting. Because some points included wetlands dominated by sedges (*Carex* spp.), we walked prescribed routes to flush and count individuals hidden by vegetation. Except for 11, 14 May 1996 and 9 May 1997 (because of bad weather and mechanical problems), we obtained a complete, daily count of all shorebirds from 26 April to 22 May 1996 and 25 April to 23 May 1997. Except for changes in observers, survey procedures were identical between years. For the three missing survey days, we used the mean of the two counts bracketing the missing day to estimate a number for each species on those days. We averaged

TABLE 1. Annual number of individuals and percentage of total for each shorebird species observed in the Seal Creek–Ahrnklin River estuary, Yakutst, Alaska, during spring 1996 and 1997.

English name	Scientific name	Annual number observed 1996	Annual number observed 1997	% obs. 1996–1997
Western Sandpiper	*Calidris mauri*	52,434	42,686	39.1
Dunlin	*C. alpina*	48,794	45,574	38.8
Long-billed and Short-billed dowitchers	*Limnodromus scolopaceus* and *L. griseus*	6159	15,179	8.8
Least Sandpiper	*Caldris minutilla*	5305	14,741	8.2
Red Knot	*C. canutus*	2406	1576	1.6
Pectoral Sandpiper	*C. melanotos*	932	103	0.8
Semipalmated Sandpiper	*C. pusilla*	1316	502	0.7
Marbled Godwit	*Limosa fedoa*	882	818	0.7
Black-bellied Plover	*Pluvialis squatarola*	373	1217	0.7
Whimbrel	*Numenius phaeopus*	119	441	0.2
Semipalmated Plover	*Charadrius semiplamatus*	222	105	0.1
Black Turnstone	*Arenaria melanocephala*	118	152	0.1
Hudsonian Godwit	*Limosa haemastica*	27	41	<0.1
Red-necked Phalarope	*Phalaropus lobatus*	22	31	<0.1
Spotted Sandpiper	*Actitis macularia*	12	33	<0.1
Greater Yellowlegs	*Tringa melanoleuca*	19	19	<0.1
Pacific Golden-Plover	*Pluvialis fulva*	15	21	<0.1
Common Snipe	*Gallinago gallinago*	7	22	<0.1
Lesser Yellowlegs	*Tringa flavipes*	4	20	<0.1
Ruddy Turnstone	*Arenaria interpres*	1	15	<0.1
American Golden-Plover	*Pluvialis dominica*	10	5	<0.1
Killdeer	*Charadrius vociferans*	—	1	<0.1

daily counts across years to determine species composition and to illustrate timing of spring shorebird migration.

We used information on the daily turnover rate of radio-tagged Western Sandpipers (Bishop, unpubl. data) to transform our daily counts into estimates of seasonal population size. From her data, 93.3% (14 of 15) of the radio-tagged Western Sandpipers located on the forelands remained there for only 1 day and 6.7% (1 of 15) remained there for 2 days. Because no explicit information exists on the turnover rates of any species other than Western Sandpipers, we assumed that the turnover rate of Least Sandpipers (*Calidris minutilla*), Semipalmated Sandpipers (*C. pusilla*), and Dunlins (*C. alpina*) would be similar to that of Western Sandpipers, therefore we combined counts of these species to yield a daily count of small calidridine sandpipers. None of these sandpipers breed in significant numbers in the estuary and our impression in the field was that their migration behaviors in the estuary were similar. Following the probabilistic approach of Butler and coworkers (1987), we used the turnover proportions to divide the daily count into the number of individuals that would stay 1 day and the number of individuals that would stay 2 days. We then calculated the number of new birds (n) on a day (t) as the daily count − $[n_{(t-1)} \times (1/15)]$ and summed the number of new birds across all days to get an annual estimate of population size; we estimated population sizes separately for 1996 and 1997.

To estimate the total number of shorebirds that used the forelands as a migration stopover, we examined aerial survey data collected on the distribution of migrant shorebirds among foreland estuaries. During spring 1980, Petersen and coworkers (unpubl. data) flew fixed-wing aircraft surveys of the forelands' estuaries every five days between 3 April and 10 May. Surveys were flown 30 m above the ground, at 130 km/hr, and shorebirds were identified and counted. We combined their counts for small calidridine sandpipers (14,092 individuals) and determined that 28.6% of the detections were made in the Seal Creek-Ahrnklin River estuary. We divided our population estimate for the Seal Creek-Ahrnklin River estuary by 28.6% to obtain an estimate of the entire spring shorebird population on the forelands. Because we surveyed only 42% of the Seal Creek-Ahrnklin River estuary, this procedure gave a conservative estimate of spring shorebird use of estuaries on the Yakutat Forelands.

RESULTS

Twenty-three species of migrant shorebirds were observed in the Seal Creek-Ahrnklin River estuary in spring 1996 and 1997 (Table 1). We recorded an additional six species on opportunistic surveys of ocean beaches adjacent to the Seal Creek-Ahrnklin River: Black Oystercatcher (*Haematopus bachmani*), Wan-

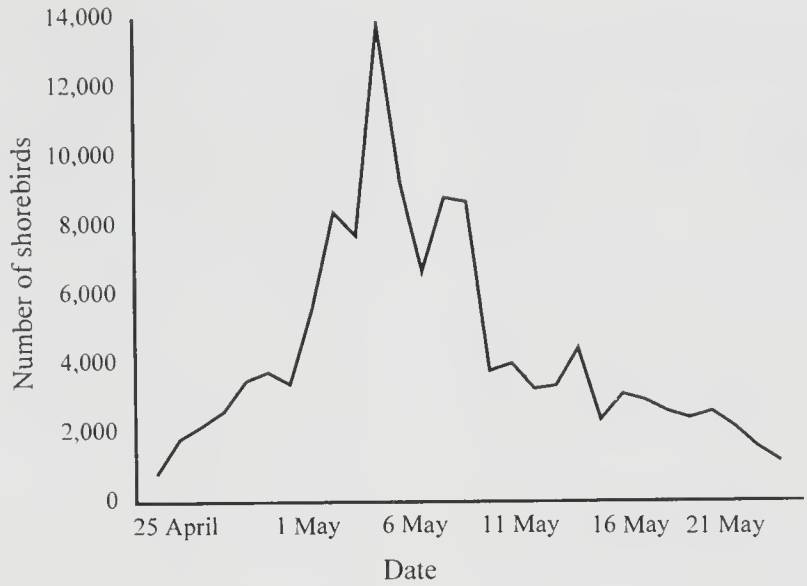

FIG. 2. Daily number of shorebirds present in the Seal Creek-Ahrnklin River estuary (averaged for 1996 and 1997) during spring migration on the Yakutat Forelands, Alaska.

dering Tattler (*Heteroscelus incanus*), Surfbird (*Aphriza virgata*), Sanderling (*Calidris alba*), Baird's Sandpiper (*C. bairdii*), and Rock Sandpiper (*C. ptilocnemis*). Small calidridine sandpipers dominated the migratory shorebird assemblage (six of the eight most abundant species), and two species, the Western Sandpiper and Dunlin, constituted 78% of all shorebird observations. Least Sandpipers, dowitchers (*Limnodromus* spp.), and Red Knots (*Calidris canutus*) also were common migrants (19% of the observations). The remaining 16 species constituted less than 4% of the shorebird observations. Marbled Godwits (*Limosa fedoa beringiae*) are rare spring migrants along the Pacific coast north of British Columbia (Kessel and Gibson 1978) and our single-day count of 358 birds on 3 May 1996 was exceptional.

Applying turnover rates to daily counts, we estimated that the small calidridine sandpiper population using the survey area in the Seal Creek-Ahrnklin River estuary was 101,300 individuals in 1996 and 100,700 individuals in 1997. Based on distribution information from the prior aerial surveys, we estimated that all estuaries on the forelands supported 354,000 (1996) and 352,000 (1997) small calidridine sandpipers during spring migration.

Shorebird numbers were highest during the first week of May (Fig. 2); daily counts exceeded 5000 individuals between 30 April and 10 May. Single-day counts exceeded 10,000 individuals on one day in 1996 (10,800 individuals on 8 May) and on two days in 1997 (19,000 individuals on 5 May and 11,400 individuals on 6 May). Numbers declined rapidly after 10 May. On the first and last surveys, 1000–2000 shorebirds were present in the study area.

DISCUSSION

Clearly, the Yakutat Forelands provides important stopover habitat for migratory shorebirds; estimates of hundreds of thousands of shorebirds were previously unreported. According to Western Hemisphere Shorebird Reserve Network abundance criteria (Harrington and Perry 1995), our estimate of a spring population of 350,000 individuals qualifies the forelands as a site of international importance (annually supports >100,000 shorebirds) to migratory shorebirds. Our estimate is most likely conservative because: (1) shorebirds were present in the estuary before and after the survey period, (2) only 42% of the Seal Creek-Ahrnklin estuary was surveyed, (3) individuals that remained on the forelands for less than one day were not considered in estimated totals, (4) shorebird use of the Ankau saltchucks was not considered (located south of the village of Yakutat; some radio-tagged birds were detected there), and (5) species other than small calidridine sandpipers were not considered in population estimates for the forelands. Accounting for any of these factors would increase our estimate of the total spring shorebird population on the forelands and

would offset any overestimate caused by assuming that migration behavior of Dunlins was similar to that of Western Sandpipers.

Counts from staging areas on the Alaska Peninsula indicate that the Pacific flyway population of Marbled Godwits is 1000–2000 individuals (Gibson and Kessel 1989). Other than the Alaska Peninsula staging areas, large aggregations of Marbled Godwits previously were unrecorded in Alaska; spring migration records from southcentral Alaska range from 1–20 individuals (Kessel and Gibson 1978). Thus, our annual estimate of about 400 individuals for the Seal Creek-Ahrnklin estuary could represent as much as 20–40% of the flyway population. Further information on the distribution of godwits among estuaries of the forelands and on the length of time they spend in the estuaries is needed to accurately assess the importance of the forelands as a migratory stopover site for this endemic Alaskan subspecies.

Composition of the shorebird assemblage on the Seal Creek-Ahrnklin River estuary was similar to the Copper-Bering River Delta; Western Sandpipers, Dunlins, Least Sandpipers and dowitchers were the most abundant species in both areas (Isleib 1979, Murphy 1981). However, Western Sandpipers and Dunlins constituted a greater proportion of all shorebird migrants on the Copper-Bering River Delta (95%) and in Kachemak Bay, Alaska (Senner et al. 1981), than at Yakutat. A greater proportion of Dunlins was observed at Yakutat than at these other southcentral Alaska sites. Although Western Sandpipers and Dunlins were also prevalent on the Fraser Delta, British Columbia, Black-bellied Plovers *(Pluvialis squatarola)* were more abundant there than at Yakutat (Butler 1994). Timing of spring migration on the forelands also was similar to the Copper-Bering River Delta and Kachemak Bay with the greatest number of shorebirds using estuaries during the first ten days of May (Isleib 1979, Murphy 1981, Senner et al. 1981). On average, individual Western Sandpipers spent much less time at stopovers on the forelands than at any other site along the Pacific Coast (Bishop, unpubl. data). This suggests that shorebirds lacking energy to reach the Copper-Bering River Delta (350 km to the northwest) use the forelands to partially replenish exhausted reserves. That many individual shorebirds were observed foraging during low tides indicated shorebirds used the estuary for more than just a rest stop. Whatever the stimuli for shorebirds to stop on the Yakutat Forelands, the magnitude of the spring shorebird migration supports Iverson's and coworkers' (1996) assertion that the conservation of Pacific Flyway populations of shorebirds depends upon a network of stopover sites. The importance of the Pacific Coast migration route to Western Sandpipers is well established (Butler et al. 1996). In the event of a major perturbation to other estuaries along the flyway, the forelands may provide critical stopover habitat to migratory shorebirds displaced from other sites. Although every site within the network may not be equally crucial to the maintenance of shorebird populations, conservation of coastal stopover sites should certainly focus on a series of well-dispersed sites that each support more than 100,000 individuals annually. Besides numerical importance, critical sites might also be defined by their functional significance to migrating shorebirds or by the effects that loss or degradation of the site would have on migratory shorebird populations (see Senner and Howe 1984).

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SHOREBIRD SURVEYS IN ENSENADA PABELLONES AND BAHIA SANTA MARIA, SINALOA, MEXICO: CRITICAL WINTER HABITATS FOR PACIFIC FLYWAY SHOREBIRDS

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ABSTRACT.—On 6–9 December 1993 and 14–18 February 1994 ground surveys of shorebirds were conducted in Ensenada Pabellones and Bahia Santa Maria, Sinaloa, Mexico. These were the first comprehensive ground surveys of shorebirds conducted in western Mexico. Twenty-nine species of shorebirds were recorded. The composition was characterized by those species spending their non-breeding period on the Pacific Coast of North America. Total numbers of shorebirds estimated were 340,063 birds (December) and 405,483 birds (February) in Ensenada Pabellones and 248,044 birds (December) and 389,841 birds (February) in Bahia Santa Maria. Western Sandpiper (*Calidris mauri*) comprised 82% of shorebirds present in both bays. American Avocet (*Recurvirostra americana*; 6% average total), dowitchers (*Limnodromus* spp.; 6% average total), and Least Sandpiper (*Calidris minutilla*; 3% average total) were also abundant. These bays hold approximately 30% of the shorebirds wintering in Pacific coastal regions of North America. Using Western Hemisphere Shorebird Reserve Network criteria, both bays are of international importance for shorebirds. Ensenada Pabellones is of regional importance for American Avocets supporting nearly 10% of the total world population. Both bays would qualify as wetlands of international importance as defined by the Ramsar Convention on international wetlands. *Received 28 Aug. 1997, accepted 18 April 1998.*

Many North American breeding birds are Neotropical migrants that move to wintering areas in South and Central America (DeGraaf and Rappole 1995, Hagan and Johnston 1992). The decline of habitats in Neotropical countries has become an international concern for both forested and wetland systems. In particular, coastal wetlands and estuaries have suffered significantly and future economic development continues to threaten these important sites of waterbird diversity (Bildstein et. al 1991). Most of North America's over 50 species of shorebirds depend on coastal wetlands in the Neotropics during the non-breeding season. Indeed, many authors have acknowledged that Nearctic breeding shorebirds are true Neotropical migrants (Rappole et al. 1983; Morrison and Ross 1989; Morrison and Myers 1987, 1989). Surveys conducted by the Canadian Wildlife Service (CWS) around all of South America identified important wintering sites for many North American breeding shorebirds (Morrison and Ross 1989). Recent efforts by the CWS (Morrison et al. 1992, 1993, 1994), combined efforts of U.S. Fish and Wildlife Service (USFWS), Point Reyes Bird Observatory (PRBO; Page et al. 1992, 1997), and Manomet Observatory for Conservation Science (MOCS; Harrington 1992, 1993, 1994) have called attention to the importance of Mexican and Central American wintering sites. Aerial surveys from 1992–1994 were used to assess and rank the importance of the coastal bays of western Mexico for wintering shorebirds (Harrington 1992, 1994; Morrison et al. 1992, 1994).

In April 1993, a field reconnaissance of the northern two-thirds of Sinaloa's coastal wetlands was conducted by Ducks Unlimited de Mexico (DUMAC) and Ducks Unlimited, Inc. (DU). This survey was part of an effort to characterize the resources of Sinaloa's coastal bays and to develop a comprehensive regional conservation plan. The April reconnaissance further revealed that aerial surveys had underestimated small shorebird numbers and did not clarify species composition. We confined

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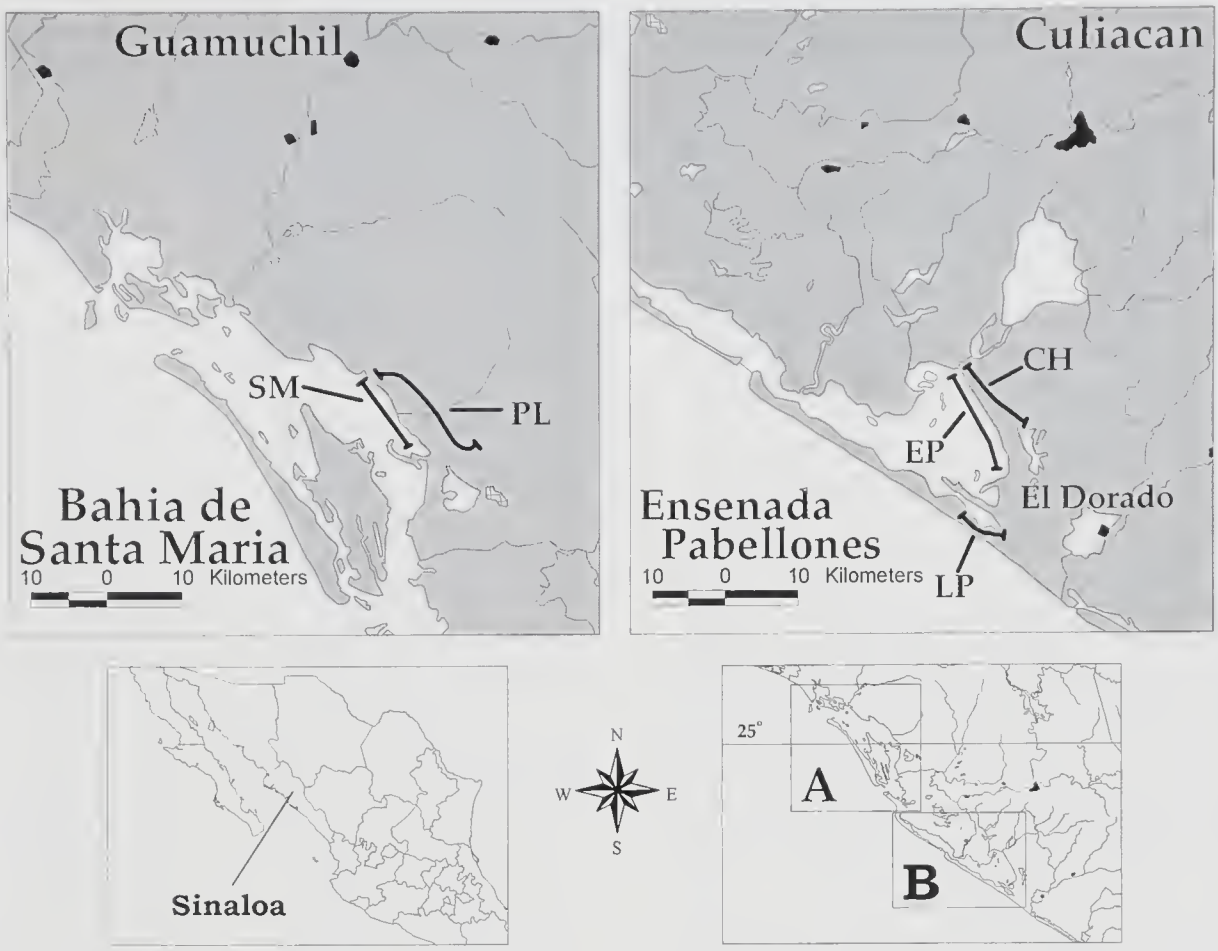

FIG. 1. Ensenada Pabellones and Bahia Santa Maria transect locations. Transect abbreviations: SM = Santa Maria, PL = Patolandia, EP = Ensenada Pabellones, CH = Chirachueto Marsh, LP = Lucenilla Peninsula.

our shorebird surveys to two bays: Bahia Santa Maria and Ensenada Pabellones (Fig. 1). These bays are important as shorebird and waterfowl stopover sites, but they are also important to the Mexican economy. Economic activities in and around the marshes is dominated by agriculture, commercial fishing, and a rapidly developing shrimp industry. The marshes also support hunting outfitters and ecotourism. Further development of these bays is planned. The aim of DUMAC's surveys has been to document the region's wildlife resources and to ensure that the conservation of these resources remains one of the priorities for future economic development. The team focused its survey efforts on the region's shorebirds to supplement the abundant waterfowl data already available for these bays (Saunders 1981, Kramer and Migoya 1989). We also documented overall avian diversity (Engilis and Carrera, in press).

STUDY AREA AND METHODS

Ensenada Pabellones.—Ensenada Pabellones is a diverse coastal estuary encompassing 800 km^2 (Scott and Carbonell 1986). Shorebirds inhabit the extensive intertidal flats (inner bay) and mangrove lined mudflats (outer bay; Fig. 1). Our reconnaissance trip on 23 April 1993 and data from MOCS and CWS surveys (Harrington 1992, 1993, 1994; Morrison et al. 1992, 1994) indicated that three regions of the bay were important for shorebirds. Transects were established in these regions.

Transect Chirachueto (CH) covered the interior marshes and estuary between uplands and mangrove edge (Fig. 1). Transect Chirachueto was 14 km long and included eight point-count stations. Water depth varied from 0–10 cm. The area was under tidal influence but remained covered by water because of slow drainage. A distinct hypopycnal zone marked the transition from freshwater to brackish water. Brackish flats were coated with algae. Emergent vegetation was characterized by *Scirpus* flats mixed with various species of sparsely growing *Spartina*, *Sesuvium*, and *Disticilis*. Intertidal zones were composed of exposed, firm mud. Floating aquatic plants were dominated by *Ruppia*. In freshwater areas where irrigation runoff entered the bay, the marsh was overgrown by stands of *Typha* and *Scirpus*. Floating vegetation included *Ruppia* and *Najas*. *Eichhornia* created large floating mats that moved with prevailing winds and tidal flow.

Transect Ensenada Pabellones (EP) covered the eastern, interior shoreline of Ensenada Pabellones. This

shoreline was 17 km long and was bounded by a ridge of mangrove (*Rhizophora* spp.) The transect was 14 km long and included eight point-count stations. Small channels through the mangroves allowed for limited exchange of tidal waters with the interior marshes of Chircahueto. The outer bay was characterized by a liquefied mud-mass more than 50 cm thick. The mud would not support a human but was passable by airboat. There was no aquatic vegetation on the flats. The mudflats were exposed to a width of 1–2 km at low tide, and were completely submerged at low tide. Mangroves were established on ridges of firm mud that ran parallel to the flats.

Transect Lucenilla (LP) covered a complex wetland zone created by dune formation on the Santa Eleana Peninsula (Fig. 1). Transect Lucenilla was 2 km long and included two point-count stations. Water in this back-dune wetland was fresh to brackish. The back-dune wetlands were highly variable from *Spartina-Disticilis-Scirpus* dominated marsh to open alkali flats. Some of the flats were lined by mangroves. The back-dune wetlands were marginally affected by tides, but water depths varied as a result of surface inflow of freshwater. The remainder of the area was covered by dense mangrove. The transect passed through habitats that have been degraded by the construction of shrimp ponds.

Bahia Santa Maria.—Bahia Santa Maria is a 1350 km^2 estuary composed of a diverse mosaic of mangrove, intertidal mudflats, freshwater marshes, extensive brackish flats, and emergent brackish marsh (Scott and Carbonell 1986). Using reconnaissance, by boat in April 1993, and by air in December 1993, we determined the placement of two transects in Bahia Santa Maria.

Transect Santa Maria (SM) covered 12 km of shoreline and included eight point-count stations. It was located along the coast south of the fishing village of La Reforma (Fig. 1). The intertidal mudflats of SM were comprised of consolidated silt and shell fragments that were capable of supporting the weight of a human. Thus, this substrate differed greatly from the unconsolidated mud of Ensenada Pabellones. The bay was surveyed on a rising tide that served to concentrate shorebirds along the water's edge. Flats of *Zostera* were evident along the shore. Otherwise, mudflats were unvegetated. Two point-count stations (SM-4 and 5) surveyed unconsolidated mud similar to that found in Ensenada Pabellones.

Transect Patolandia (PL) covered the interior marshes characteristic of Bahia Santa Maria, was 18 km long, and had five point-count stations. Habitats at these stations ranged from open, algae covered mudflats with a water depth of 4 cm to sparsely vegetated areas with water 4–20 cm deep. Dominant vegetation included *Scirpus, Salicornia, Atriplex,* and *Chenopodium.* Freshwater intrusion into the bay from agricultural runoff is transforming interior marshes to dense stands of *Typha.* The upper arms of the bay were already fully overgrown with *Typha.* A salt mining operation exists in the bay's southern reach.

Survey period and methods.—Transects were selected and established to cover intertidal flats and interior marshes, areas that received minimal coverage from MOCS and CWS aerial surveys. The three transects (18 point-count stations) at Ensenada Pabellones were surveyed on 8–9 December 1993 and 14–15 February 1994, while the two transects (13 point-count stations) in Bahia Santa Maria were surveyed on 6–7 December 1993 and 16–17 February 1994. Point-count stations were located through the use of a Trimble global positioning system device (GPS) and coordinates recorded using the UTM system. The coordinates of these data points are available from Ducks Unlimited's Western Regional Office. Airboats were used to access transects and point-count stations. The survey team was comprised of a crew member to operate the boat and at least two trained observers. Surveyors used 8× and 10× binoculars and 22× spotting scopes.

Because it was not possible to count each shorebird, we developed a sampling regime designed to estimate the number of birds present on transects. The sampling regime had two parts: (1) point counts were conducted along each transect at which birds within a 400 m circle were identified to species and counted; (2) we estimated the total number of birds along each transect line, including areas between points (to a width of 200 m). The number estimated on the transect was developed using the combined point count totals for each species as a percentage of the total birds we estimated along the transect. Thus, if we counted 50,000 birds of a given species on point counts, and that number represented 50% of the total estimated on the transect, we reported 100,000 birds for the transect. These percentages are expressed for each species in Tables 1 and 2. All stations were censused during each survey period. Each transect was characterized by habitat indicating substrate, dominant vegetation, and water depth. Where species identification was impossible, shorebirds were grouped to genus (e.g., *Calidris, Limnodromus*). Numbers of shorebirds were determined by direct counts or by flock estimations when larger concentrations were encountered. Count data were recorded onto tape recorders and transcribed to field forms. These counts were not time dependent.

The April 1993 reconnaissance revealed that airboats caused shorebirds to take flight as they approached. To minimize this problem we adopted the following protocol on all subsequent surveys. A count station was always approached at an angle perpendicular to the transect line, minimizing disturbance. When a count was completed, the airboat was driven 0.5 km away (perpendicular) from, and then parallel to the transect line, until we reached the approach for the next count station. We then turned the airboat towards the next station allowing the airboat to coast to a stop with the engine turned off. The engine was only turned on to move the boat between stations; it was not on during the survey period. The GPS units allowed us to predict when to start our approach to each station and when to turn off the engine. This tactic resulted in reduced disturbance to birds.

TABLE 1. Shorebird survey results Ensenada Pabellones.

Species		% of birds counted on transects[a]	December 1993		February 1994	
			Number counted	Total estimated	Number counted	Total estimated
Snowy Plover	*Charadrius alexandrinus*	60%	63	105	54	90
Semipalmated Plover	*Charadrius semipalmatus*	60%	174	290	109	182
Killdeer	*Charadrius vociferus*	20%	8	40	17	85
Wilson's Plover	*Charadrius wilsonia*	60%	5	8	2	2
Black-bellied Plover	*Pluvialis squatarola*	40%	289	723	37	93
American Oystercatcher	*Haematopus palliatus*	—	—	—	2	2
Black-necked Stilt	*Himantopus mexicanus*	20%	367	1835	638	3190
American Avocet	*Recurvirostra americana*	40%	15,702	39,255	11,792	29,480
Spotted Sandpiper	*Actitis macularia*	—	2	2	1	1
Sanderling	*Calidris alba*	—	—	—	45	45
Red Knot	*Calidris canutus*	20%	200	1000	40	200
Stilt Sandpiper	*Calidris himantopus*	30%	48	160	311	1037
Dunlin	*Calidris alpina*	60%	417	695	30	150
Western Sandpiper	*Calidris mauri*	30%	82,767	275,890	99,906	333,020
Least Sandpiper	*Calidris minutilla*	30%	3235	10,783	61	203
Willet	*Catoptrophorus semipalmatus*	40%	349	873	313	782
Common Snipe	*Gallinago gallinago*	—	—	—	2	2
Dowitcher species	*Limnodromus* spp.	—	—	—	12,450	20,750
Short-billed Dowitcher	*Limnodromus griseus*	60%	1928	3213	450	750
Long-billed Dowitcher	*Limnodromus scolopaceus*	60%	2028	3380	7978	13,297
Marbled Godwit	*Limosa fedoa*	50%	729	1458	953	1906
Long-billed Curlew	*Numenius americanus*	20%	18	90	4	20
Whimbrel	*Numenius phaeopus*	20%	40	200	16	80
Lesser Yellowlegs	*Tringa flavipes*	50%	21	42	44	88
Greater Yellowlegs	*Tringa melanoleuca*	50%	10	20	14	28
Red-necked Phalarope	*Phalaropus lobatus*	—	1	1	—	—
Total			108,401	340,063	135,269	405,483

[a] Percentage reflects the number of birds counted on stations in relation to the number of birds estimated on the transect (e.g., the 82,767 Western Sandpipers counted on stations represent 30% of the total estimated on the transect).

Relative abundance (% composition) was calculated for each species. Since Western Sandpipers (*Calidris mauri*) outnumbered all others, relative abunance was expressed both with Western Sandpiper numbers included in the total and omitted from the total.

RESULTS

At Ensenada Pabellones, 108,401 individuals of 22 shorebird species were counted at point count sites in December 1993. The total number of birds along transects was estimated to be 340,063 (Table 1). In February 1994, 135,269 individuals of 24 shorebird species were counted; 405,483 were estimated along transects. During both surveys, Western Sandpiper was the most abundant species followed by American Avocet (*Recurvirostra americana*), dowitchers (*Limnodromus* spp.), and Least Sandpiper (*Calidris minutilla*). In December, Ensenada Pabellones accounted for 58% of the shorebirds surveyed in both bays; in February 51%.

At Bahia Santa Maria, 78,259 individuals of 24 shorebird species were counted on survey points in December 1993. The total number of birds along transects was estimated to be 248,044 (Table 2). In February 1994, 130,657 individuals of 24 shorebird species were counted on survey points; 389,841 were estimated on transects. During both surveys, Western Sandpiper was the most numerous species followed by dowitchers, Least Sandpipers, Dunlin (*Calidris alpina*), and American Avocets. The species are summarized below in order of abundance.

The Western Sandpiper was the most abundant shorebird in both bays and in both count periods. They comprised 80% of all shorebirds identified in both bays. Considering the

TABLE 2. Shorebird survey results Bahia Santa Maria.

Species		% of birds counted on transects[a]	December 1993		February 1994	
			Number counted	Total estimated	Number counted	Total estimated
Snowy Plover	*Charadrius alexandrinus*	20% Dec, 60% Feb	11	55	222	370
Semipalmated Plover	*Charadrius semipalmatus*	60%	10	17	44	73
Killdeer	*Charadrius vociferus*	20%	14	70	14	70
Wilson's Plover	*Charadrius wilsonia*	60%	50	83	18	30
Black-bellied Plover	*Pluvialis squatarola*	60%	262	437	45	75
American Oystercatcher	*Haematopus palliatus*	—	4	4	3	3
Black-necked Stilt	*Himantopus mexicanus*	20%	823	4115	571	2855
American Avocet	*Recurvirostra americana*	60%	1036	1727	3889	6482
Spotted Sandpiper	*Actitis macularia*	—	4	4	2	2
Ruddy Turnstone	*Arenaria interpres*	20%	88	440	83	415
Sanderling	*Calidris alba*	60%	2468	4113	36	60
Red Knot	*Calidris canutus*	20%	341	1705	133	665
Stilt Sandpiper	*Calidris himantopus*	60%	404	673	482	803
Western Sandpiper	*Calidris mauri*	30%	60,547	201,823	99,530	331,767
Least Sandpiper	*Calidris minutilla*	30%	6479	21,597	855	2850
Willet	*Catoptrophorus semipalmatus*	40%	861	2153	1958	4895
Common Snipe	*Gallinago gallinago*	—	2	2	—	—
Dowitcher species	*Limnodromus* spp.	60%	—	—	14,437	24,062
Short-billed Dowitcher	*Limnodromus griseus*	60%	902	1503	503	838
Long-billed Dowitcher	*Limnodromus scolopaceus*	60%	2760	4600	7087	11,811
Marbled Godwit	*Limosa fedoa*	50%	1014	2028	670	1340
Long-billed Curlew	*Numenius americanus*	20%	54	270	29	145
Whimbrel	*Numenius phaeopus*	20%	60	300	25	125
Lesser Yellowlegs	*Tringa flavipes*	20%	21	105	3	15
Greater Yellowledgs	*Tringa melanoleuca*	20%	44	220	18	90
Total			78,259	248,044	130,657	389,841

[a] Percentage reflects the number of birds counted on stations in relation to the number of birds estimated on the transect (e.g., the 60,547 Western Sandpipers counted on stations represent 30% of the total estimated on the transect).

widespread distribution of this species, and the limited coverage of our transects, our estimate of over 600,000 birds should be considered a minimum number. Our April 1993 estimate of 1,000,000 *Calidris* sandpipers (850,000 westerns) indicates that these bays also support Western Sandpiper through their migration period. Western Sandpipers foraged predominantly in shallow water of open and semi-open flats. They exhibited the widest variety of substrate use, and were one of the few species that regularly exploited algal flats. Western Sandpipers characteristically foraged in dense flocks, some numbering 25,000 birds or more. Frequently they were joined by other *Calidris* species. Flocks of Western Sandpipers regularly flew between interior wetlands and intertidal flats, moving to the intertidal habitats during low and receding tides. Interior wetlands were the preferred roost sites for Western Sandpipers.

American Avocets were concentrated, often in large aggregations, on the eastern shoreline of Ensenada Pabellones. Birds foraged in liquefied mud, particularly along the receding or increasing tidal water edge. Peak estimated numbers at Ensenada Pabellones exceeded 39,000 birds (Table 1). Avocets were also counted in Chircahueto Marsh loafing in flocks on exposed mudflats, particularly at high tide. Some birds foraged along the edges of the interior marsh on flooded mudflats. Peak counts in this interior area exceeded 4000 birds (December). Avocets were not as abundant in Bahia Santa Maria. They were concentrated on the bay's interior, marsh-lined mudflats. They avoided the consolidated silt-shell flats characteristic of the eastern shoreline, but frequented liquefied mud at point-count stations SM7 and SM8 (off shore from La Reforma). Avocets were not found on the algal covered, intertidal flats characteristic of

Bahia Santa Maria. Peak counts in Bahia Santa Maria exceeded 6400 birds (February survey period). American Avocets were one of three co-dominant species with a relative abundance of 5–7% in both bays. When compared to other shorebirds but omitting Western Sandpiper counts, relative abundance was 28–38%.

Dowitchers of both species were found in both bays. They sorted themselves between habitats in December. Short-billed Dowitchers (*Limnodromus griseus*) occurred primarily on intertidal flats of consolidated and liquefied mud while Long-billed Dowitchers (*L. scolopaceus*) occurred in the shallow flooded, interior wetlands along the margins of small flats, ponds, channels and bays. The latter species infrequently visited intertidal flats. In February, this pattern changed. Census totals jumped from 12,000 birds in December (combined species in both bays) to nearly 70,000 birds (combined species in both bays; Tables 1, 2). In February dowitchers no longer sorted themselves between habitats as both species frequented intertidal flats. During February we had to count birds to "dowitchers only." Dowitchers were another co-dominant shorebird representing 2% of the total birds surveyed in December and 9% in February. When relative abundance is compared between all shorebirds, omitting Western Sandpiper numbers, dowitchers represented 11% in December and 57% in February.

Least Sandpipers were distributed in linear bands of mudflat along vegetated margins. This spacing and distribution made accurate surveys of this species difficult. In some instances, especially where water depths were 2–4 cm or less, Least Sandpipers were mixed with Western Sandpipers, but their numbers varied. For example, on 6 December 1993 at Station PL3, we observed 4700 Least Sandpipers with 39,000 Western Sandpipers and 2400 Dunlin. On 16 February 1994, this same station yielded 74,000 Western Sandpipers and only 815 Least Sandpipers and 10 Dunlin. Least Sandpipers comprised nearly 6% of total birds in both bays in December 1993. The February surveys counted only 3000 birds. The 10 fold decline may be the result of birds migrating north, or moving to other areas of the bays.

Black-necked Stilts (*Himantopus mexicanus*) were evenly distributed throughout the interior wetlands, frequenting mudflats and shallow flooded habitats of both bays. They were usually observed in pairs, rarely in large aggregations. At Ensenada Pabellones, stilts were most numerous in the shallow interior brackish flats and freshwater ponds and channels of Lucenilla and Chircahueto marshes. They were rare in the liquefied mud substrate in Ensenada Pabellones during both survey periods. Peak numbers exceeded 3000 birds in Ensenada Pabellones (Table 1). In Bahia Santa Maria, stilts frequented the vegetated interior wetlands, channels, and ponds. They were also found on the shallow inundated silt-shell substrate and liquefied mud near La Reforma. Peak counts in Bahia Santa Maria exceeded 4100 birds (Table 2). Stilts had a relative abundance of 1% in both bays in December. When Western Sandpiper counts were removed from calculated totals, stilts comprised 5% of total birds.

Stilt Sandpipers (*Calidris himantopus*) were regularly counted in all interior wetland habitats. They associated with other *Calidris* and dowitchers. Because of their tendencies to be interspersed with other species, our point-counts included only 30% of the total estimated to occur along the transects. Stilt Sandpipers foraged in shallow water on mud or algal covered flats. They preferred flooded areas and were infrequently observed on intertidal margins. Stilt Sandpipers represented 1% of all shorebirds (excluding Western Sandpiper numbers).

Marbled Godwits (*Limosa fedoa*) were mostly restricted to intertidal flats. They were evenly distributed across a wide range of substrates from consolidated flats to liquefied flats along the water's edge. Chiriaqueto marshes provided a significant roost site for godwits foraging in Ensenada Pabellones. Godwits were equally distributed between bays. We estimated over 10,000 godwits in Bahia Santa Maria and over 1000 birds in Chiriaqueto marshes during the April 1993 survey. Godwits comprised 3% of total shorebirds (excluding Western Sandpiper numbers).

Willets (*Catoptrophorus semipalmatus*) were most abundant on the eastern shoreline of Bahia Santa Maria where they were restricted to consolidated intertidal flats. This reach of the bay contained 70–85% of the to-

tal Willets in both bays. In April, 1993 we estimated 2000 Willets along Santa Maria's eastern shore. Willets comprised 3–4% relative abundance counted in both bays (excluding Western Sandpiper numbers).

The following species represented less than 1% relative abundance, but were regularly encountered.

Six species of banded plovers were observed in both bays. One individual Collared Plover (*Charadrius collaris*) was observed 24 April 1993 at Chircahueto Marsh. Snowy Plover (*Charadrius alexandrinus*) and Semipalmated Plover (*Charadrius semipalmatus*) were common on small alkali flats of the Lucenilla Peninsula (Transect LP). Snowy Plovers also were present along the beach front of Lucenilla. Semipalmated and Snowy plovers were observed on exposed, interior wetlands in Bahia Santa Maria. Wilson's Plovers (*Charadrius wilsonia*) were documented on Lucenilla Peninsula as well as on exposed, consolidated mudflats of Bahia Santa Maria. Killdeer (*Charadrius vociferus*) were recorded in small numbers along the margins of the interior marshes, and occasionally on consolidated tidal flats.

Black-bellied Plovers (*Pluvialis squatarola*) were present and sparsely dispersed along the margins of intertidal flats, often in association with Willets and Marbled Godwits. We found no roosting concentrations of Black-bellied Plovers. They were most often found on consolidated mudflat substrates and along mangrove margins.

Dunlin were irregularly encountered during our surveys. When observed they were in flocks with other *Calidris*. Dunlin were mostly observed foraging on shallow, open mudflats of interior wetlands. They were infrequent on algal covered flats and intertidal, liquefied mudflats. In April 1993, we estimated over 10,000 Dunlin at Bahia Santa Maria indicating that this bay supports spring transients that probably winter farther south.

Red Knots (*Calidris canutus*) made extensive use of ocean strand habitats, making our estimates of this species relatively inaccurate. Knots occurred primarily on silt-shell consolidated substrate of Bahia Santa Maria (over 1700 birds). We also encountered a sizable number on mangrove margin mudflats at Ensenada Pabellones (1000 birds). During winter surveys knots infrequently were observed on interior wetlands. However, on 23 April 1993 we observed over 1000 knots in breeding plumage on the interior marshes of Chircahueto.

Whimbrels (*Numenius phaeopus*) and Long-billed Curlews (*Numenius americanus*) occurred in small numbers in both bays. They were restricted to the higher, consolidated intertidal flats and mangrove edge, being evenly distributed along the margins of both bays. The reclusive behavior of curlews, ducking into the mangrove when frightened, made estimating their numbers difficult. However, they clearly were not abundant in either bay during winter. Whimbrels were more abundant during the April 1993 survey, when over 1000 birds were observed in Bahia Santa Maria.

DISCUSSION

U.S. Fish and Wildlife surveys and banding recoveries have shown that most waterfowl wintering in western Mexico originate and move through traditional "Pacific Flyway" corridors (Kramer and Migoya 1989, Saunders 1981). Over 250,000 Nearctic nesting ducks annually occur in the bays of Sinaloa during the non-breeding season (Kramer and Migoya 1989). Although banding evidence is lacking for shorebirds, the high numbers of non-breeding Western Sandpipers, dowitchers, and avocets and the lack of Semipalmated (*Calidris pusilla*), Baird's (*Calidris bairdii*) and White-rumped (*Calidris fuscicollis*) sandpipers are more characteristic of Pacific Coast species aggregations (Helmers 1992, Page et al. 1992, Jehl 1994, Page and Gill 1994).

We recorded 29 species of wintering shorebirds during our surveys (Tables 1, 2). In comparison, 24 species winter in San Francisco Bay (Harvey et al. 1992), 22 species winter in California's Central Valley (Shuford et al. 1994), and 27 species winter in coastal bays of Baja California (Page et al. 1997). This high diversity of shorebirds wintering in Sinaloa emphasizes the global importance of the region for western Nearctic nesting shorebirds.

Numerous authors have summarized the Pacific Flyway population of shorebirds (Palacios et al. 1991; Page et al. 1992, 1997; Page and Gill 1994; Gill et al. 1994) and while Baja California was identified as an important win-

TABLE 3. Comparison of survey results for shorebirds surveyed in the Pacific Coast of North America (winter survey results).

Location	Total shorebirds	American Avocets	Western Sandpiper	Dowitchers
California interior[a]	207,000	4038	2736	77,764
California Coast[b]	570,000	24,000	195,000	25,000
Baja California[c]	355,000	1500	127,000	48,000
Sonora Coast[d]	292,000	32,500	92,800[e]	8200
Northern Sinaloa Coast[d]	118,000	21,270	50,600[e]	6600
Bahia Santa Maria (1993)	390,000	6400	332,000	36,000
Ensenada Pabellones (1993)	405,000	29,500	333,000	34,500

Sources: [a] Shuford et al. 1994; [b] Page et al. 1992, [c] Page et al. 1997, [d] Harrington 1993.
[e] Includes all small *Calidris* spp.

tering area in Mexico, Sinaloa and Sonora wetlands generally were overlooked. CWS and MOCS surveys correctly identified the bays of Sonora and Sinaloa as among the most critical wintering habitats in Mexico for Pacific Flyway shorebirds (Morrison et al. 1992, 1994; Harrington 1992, 1993, 1994). With over 795,000 shorebirds estimated on our ground surveys, Ensenada Pabellones and Bahia Santa Maria apparently support nearly one-third of the shorebirds wintering in the North American portion of the Pacific Flyway (Table 3). Combined with Sonora's coastal bays and the remaining bays of Sinaloa (Topolobampo and Navachiste), the west coast of Mexico may well support over half of the shorebirds wintering on the Pacific Coast of North America.

Bahia Santa Maria and Ensenada Pabellones are sites of great importance to North American shorebirds in general, and both clearly exceed criteria of the Western Hemisphere Shorebird Reserve Network for classification as International Sites (i.e., host to >100,000 shorebirds). These bays may be elevated to sites of Hemispheric importance (i.e., host to >500,000 shorebirds) if more comprehensive surveys are undertaken.

Previous attempts to count shorebirds in western Mexico have been from the air only. Aerial surveys are most accurate in estimating moderate to high numbers of large, conspicuous and relatively clumped birds. Yet the value of estimates may vary as a result of factors such as species mobility and seasonal habitat conditions. For example, MOCS and CWS surveys have documented large numbers of avocets at Marismas Nationales, 220 km south of the study area (R. I. G. Morrison, pers comm.). Given the high mobility of avocets, it is not unreasonable to expect movements of birds between Marismas and coastal Sinaloa bays (Robinson and Oring 1996). On the other hand, Harrington (1993) estimated only 528 Black-necked Stilts at Bahia Santa Maria and 8 at Ensenada Pabellones, whereas we estimated 4115 and 1835 along our transects in December and 2855 and 3190 in February. Furthermore, we believe that our census of this species also underestimated the numbers present. Clearly, aerial surveys were inadequate for counting stilts because of their wide dispersion in vegetated habitats. Our survey techniques did not adequately document the abundance of Killdeer and probably underestimated all species of banded plovers. Specialized counts focusing on *Charadrius* plovers need to be adopted to assess the importance of these bays as wintering and breeding habitats.

Our data suggest that the accuracy of aerial surveys is poor for widely dispersed species, especially those inhabiting areas far from the shoreline, such as Black-necked Stilts, plovers, and yellowlegs. In addition, aerial accuracy may be low when huge numbers of birds are present, especially when they are not linearly distributed; for example, Western Sandpipers at Bahia Santa Maria. We urge investigators to take advantage of broad coverage achieved by aerial surveys to delineate critical areas for more intensive ground surveys.

Our coverage was admittedly limited, i.e., surveys once each in December 1993 and February 1994, following a preliminary visit in April 1993. However, even such cursory

coverage revealed interesting seasonal variation worthy of additional study. For example, totals of Western Sandpipers for the two bays combined, increased from 478,000 in December to 665,000 in February. Does this reflect early departure from areas south of Sinaloa, local movements, or census error? Considering that *Calidris* numbers peak on the western coast of the U.S. in mid-April (Page et al. 1979), our high April estimates beg further investigation of migration patterns of Western Sandpipers. American Avocets were perhaps our most accurately censused species. Our counts declined from 41,000 in December to 36,000 in February. Avocets begin arriving on their Great Basin breeding grounds by late February, but a decline of just 12% might reflect census error as well as early migration or local movement (L. Oring, pers. obs.).

Perhaps the most dramatic variation from December to February was shown by Least Sandpipers, declining from 32,000 to 3000, nearly a 90% drop. Did they continue farther south of Sinaloa in mid-winter? Were they already headed north in February? On the other hand, dowitchers increased from 10,000 in December to over 70,000 in February, and Willets from about 2000 to 6000. These numbers probably reflect the early stages of spring migration.

We hope that our data will pique the interest of shorebird biologists to initiate detailed studies of Neotropical migrant shorebirds along their migratory paths. Despite the preliminary nature of our findings, we urge authorities in Mexico charged with managing coastal wetlands to move now to protect what clearly is one of the most important shorebird resources on Earth. Already competing economic development has moved into both bays. Continued destruction would be a biological tragedy of enormous proportion and could have devastating effects to the Neotropical migratory shorebirds of the Americas.

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HOME RANGE AND HABITAT OF BREEDING FLAMMULATED OWLS IN COLORADO

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ABSTRACT.—We used radiotelemetry to determine habitat use by Flammulated Owls (*Otus flammeolus*) during the breeding season on 452 ha of montane conifer forest in central Colorado in 1982–1983. Mean size and SD of home ranges was 11.1 ± 1.9 ha (range = 8.5–12.5 ha, n = 4) in 1982 and 18.3 ± 5.1 ha (range = 14.0–24.0 ha, n = 3) in 1983. Habitat use by nesting males was affected by distribution of old forests of ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*), by topography, and by juxtaposition of home ranges of conspecifics. In spring, both new and returning owls settled into areas containing more old ponderosa pine/Douglas-fir than in other overstory types available in the study area. After settling, males foraged significantly more often in old ponderosa pine/Douglas-fir than in other overstory types available within home ranges. Eighty-one percent of foraging locations by males occurred in one to four intensive foraging areas within each home range. Mean size of intensive foraging areas was 0.5 ± 0.4 ha (range = 0.1–1.4 ha). Eighty percent of intensive foraging areas consisted entirely of old ponderosa pine/Douglas-fir. Use of this overstory type by Flammulated Owls is probably related to its composition and structure, and prey availability.
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When settling into landscapes birds must distinguish among available habitats, each of which may differ in quantity and quality of requisite resources (Fretwell and Lucas 1970). Habitat selection during settling likely involves an hierarchically-ordered series of choices during which a bird selects a geographic area (first-order), types of habitat in which the territory is established (second-order), and specific microhabitats for activities such as nesting, foraging, and roosting (third-order; Johnson 1980). At each order of selection a species may use different criteria for discriminating among available habitats. Western Kingbirds (*Tyrannus verticalis*), for example, may select territories on the basis of maximum canopy height, and nest-sites (microhabitats) on the basis of tree characteristics (Bergin 1992). Habitats selected at each order are limited by the preceding choice because movements of breeding birds are energetically limited to some finite area around nests. Descriptions of habitat are therefore scale-dependent (Wiens 1986, Kotliar and Wiens 1990) and focusing on a single order may preclude discerning patterns at other orders (Maurer 1985). Understanding a species' habitat selection requires the consideration of choices at each scale.

The breeding range of Flammulated Owls (*Otus flammeolus*) is from the Rocky Mountains to the Pacific Coast Mountains (except Oregon and Washington) and from south-central British Columbia to Veracruz, Mexico (McCallum 1994). Flammulated Owls are migratory and may winter from the southern United States to as far south as El Salvador (Phillips et al. 1964, American Ornithologists' Union 1983). Habitats within home ranges of Flammulated Owls have not been compared to habitats available within landscapes. Nesting Flammulated Owls have been reported in yellow pine [subsect. *Ponderosae* (Critchfield and Little 1966)] and mixed-conifer forests. These forests were often mixed with oak (*Quercus* sp.) or pinyon (*Pinus edulis*) at lower elevations, and fir (*Abies* sp.), Douglas-fir (*Pseudotsuga menziesii*), or quaking aspen (*Populus tremuloides*) at higher elevations (e.g., Marshall 1957, Bull and Anderson 1978, Richmond et al. 1980, Goggans 1986, Reynolds and Linkhart 1987, McCallum and Gehlbach 1988). Nesting Flammulated Owls were occasionally found in pinyon (Huey 1932) and Douglas-fir forests (Howie and Ritcey 1987, Powers et al. 1996).

We determined habitat selection by Flammulated Owls at multiple scales by comparing forests within owl home ranges to forests

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available in a landscape, and by comparing the owls' use of forest types and ages to availability of these within owl home ranges. We also describe the size, shape, and juxtaposition of nesting home ranges, and the species and age of trees used by the owls during foraging, territorial singing, day-roosting, and resting.

STUDY AREA AND METHODS

We established boundaries of the 452 ha study area on the Manitou Experimental Forest, Teller Co., Colorado during initial surveys (1980) for territorial Flammulated Owls. After we confirmed the presence of owls, boundaries were arbitrarily drawn around an area large enough to contain approximately 20 territorial males, based on an estimate of territory size for this species (274 m in diameter; Marshall 1939). We then conducted searches for territorial males and their nests (Reynolds and Linkhart 1984) within the boundaries from 1981–1983. Forests within the study area consisted of (1) ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir, generally on ridgetops and south and west facing slopes, (2) quaking aspen stands on lower slopes and bottoms of moist drainages, (3) quaking aspen stands mixed with blue spruce (*Picea pungens*) in bottoms, lower slopes, and benches in moist areas, and (4) Douglas-fir mixed with blue spruce, on higher slopes in drainages and on north facing slopes. Tree cutting on the study area had not occurred since the 1880s, when cuts were made for railroad ties. Snags and trees with cavities were relatively abundant throughout the study area (Reynolds et al. 1985). The forest understory, consisting of over 100 species of grasses, forbs, and shrubs, was poorly developed in all but the moist creek bottoms (Reynolds et al. 1985). Terrain was moderately steep (20–80% slope) and elevations ranged from 2550–2855 m. Annual precipitation was 40–45 cm. Daily high temperatures from June to September averaged 19° C and low temperatures averaged 5° C (Reynolds and Linkhart, unpubl. data). The study area was imbedded within forests composed of a similar mix of overstory types and ages.

We conducted the study from mid-May (pair formation) to late July (fledging of young) in 1982 and 1983. Movements and behaviors of owls after fledging of young were reported by Linkhart and Reynolds (1987). Male owls were captured at nests, banded with U.S. Fish and Wildlife Service leg bands, and equipped with tail-mounted or backpack-mounted radio transmitters (Reynolds and Linkhart 1984). Transmitter mass was 2.3–2.6 g, 4–5% of adult mass (male $\bar{x}$ = 55 g, n = 27; Reynolds and Linkhart 1987), and we detected transmitter signals up to 800 m. During the two study years, nine males nested on the study area and we studied seven of these with telemetry. One male (A4-82) was not radio-tagged because his nest was inaccessible, and another male (A24-83) abandoned his nest before he could be captured. Portions of the home ranges of five additional males occurred on the periphery of the study area; behavior of these males indicated they were not nesting (Reynolds and Linkhart 1987) and none was radio-tagged.

TABLE 1. Number of locations associated with four activities of seven radio-tagged Flammulated Owls in Colorado, 1982–1983.

	Activity				
Home range	Foraging	Day-roosting	Territorial singing	Resting	Total locations
A10-82	25	9	8	0	42
A15-82	27	9	9	2	47
A24-82	35	12	3	8	58
A29-82	35	5	10	5	55
A4-83	36	31	39	0	106
A11-83	42	20	9	5	76
A29-83	21	26	23	4	74
Total	221	112	101	24	458

We radio-tagged males after egg-laying (early June). Prior to using telemetry, we recorded locations of males observed in territorial song. We monitored the movements and behaviors of radio-tagged males by following them with a handheld radio-receiver and yagi antenna. When we first visually located a radio-tagged male, we assigned his behavior to one of the following activities: foraging, territorial singing, day-roosting, or resting. We defined foraging as an observed attempt by an owl to capture prey. Foraging attempts were nearly always followed by prey deliveries to nests (see below). We observed each owl's behavior for 1–3 h at a time, aided by flashlight or by silhouetting the owl against the sky. A stationary observer equipped with a two-way radio at the nest of the focal owl reported arrival, departure, and flight direction of the departing owl to a similarly-equipped mobile observer (always Linkhart).

In 1982, we monitored the movements of four nesting males during 52 h of observation (36% between 20:00–21:59 MST; 44% between 22:00–23:59; 20% between 24:00–01:59). In 1983, we monitored the movements of three nesting males during 45 h (40% between 20:00–21:59; 47% between 22:00–23:59; 13% between 24:00–01:59). During the two years, we recorded a total of 458 locations—202 locations in 1982 and 256 locations in 1983 (Table 1).

We mapped and plotted all foraging, territorial singing, day-roosting, and resting locations of males on aerial photographs (scale 1:1000) of the study area. Home ranges of owls were determined with the minimum convex polygon (MCP; Mohr 1947) and the area within home ranges was determined with a planimeter. On occasion, radio-tagged males intruded into the home ranges, often to the nests, of neighboring pairs (Reynolds and Linkhart 1990). We excluded these extra-range movements from the MCP determination of home ranges. To determine the sufficiency of our radio-telemetry sampling, we plotted the cumulative MCP area, using five sequential locations at a time, against the number of locations for each radio-tagged

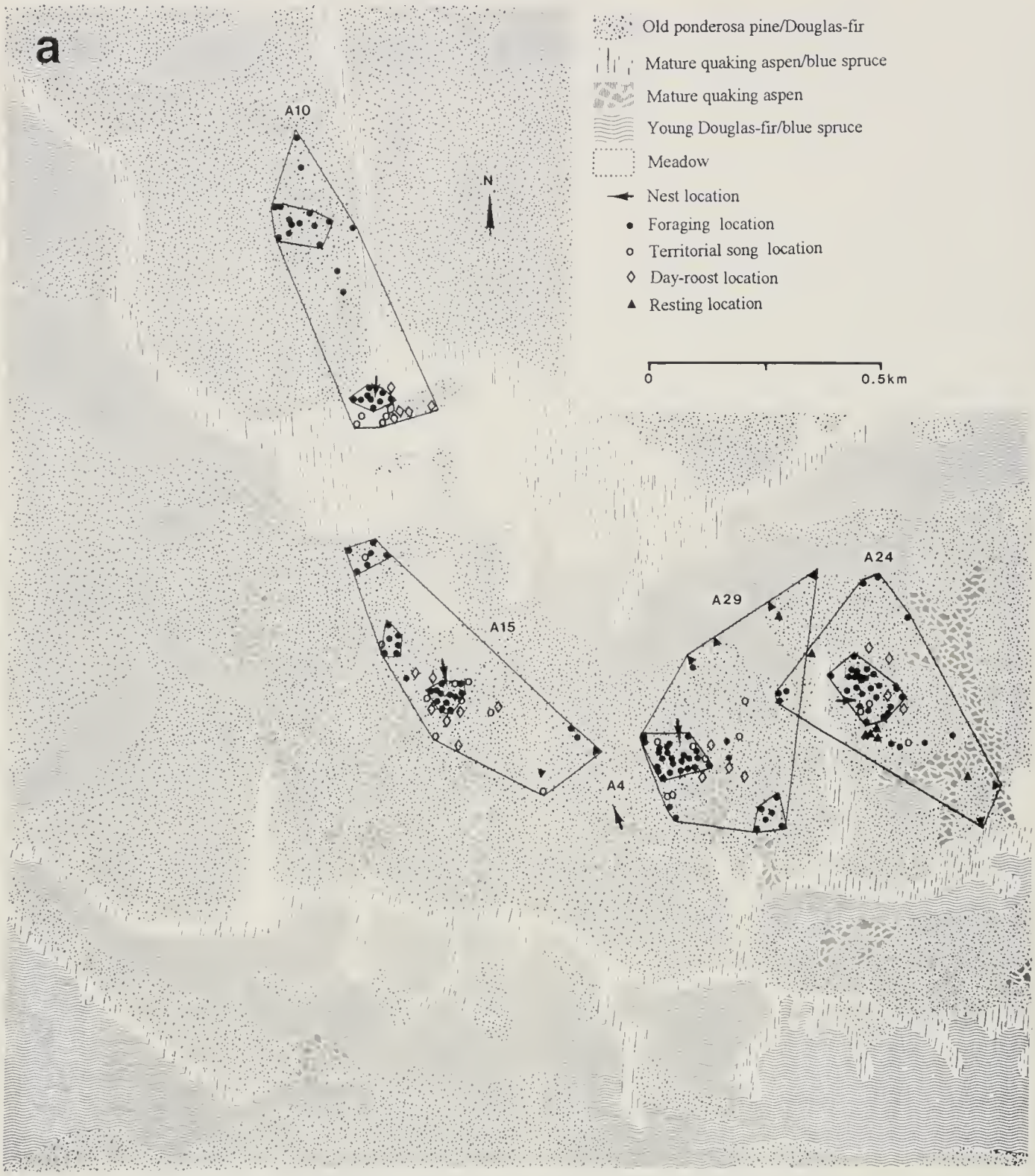

FIG. 1. Home ranges, intensive foraging areas (enclosed areas within home ranges), nests, and radio-telemetry locations of Flammulated Owls with respect to overstory types in (a) 1982 and (b) 1983. The study area is the entire area shown.

male. Asymptotes in these plots were attained in 30–80 locations (Linkhart 1984).

Five vegetation types, distinguished by overstory species, occurred in the study area: old (200–400 years) ponderosa pine/Douglas-fir; mature (100–200 years) quaking aspen/blue spruce; mature (75–125 years) quaking aspen; young (<100 years) Douglas-fir/blue spruce; and meadow. We estimated age of overstory trees by aging (with increment borer) 130 representative overstory trees, selected approximately proportional to the area of each overstory type on the study area. We delineated areas of an overstory type greater than 0.1 ha on the aerial photographs of plotted locations, and determined total area of each type with a planimeter. We then summed foraging locations in each overstory type.

FIG. 1. Continued.

We examined the owls' choices of habitat at the second-order of selection (establishment of home range) by comparing the proportional area of overstory types within home range boundaries to the proportional area of types available within the study area. For this comparison, we established 95% confidence intervals on the mean proportions of each overstory type within the seven home ranges. Our investigation of the owls' third-order habitat selection focused on habitats used for foraging. We determined choice of overstory type for foraging by comparing the proportional use of overstory types by owls to the availability of types within home ranges. Selection for overstory types was determined with a χ^2 goodness-of-fit test and Bonferroni simultaneous intervals (Neu et al. 1974). We lumped locations for all males (n = 7) for the preference analysis because number of locations of each male was insufficient for individual analyses. An attempt to use compositional analysis (Aebischer et al. 1993) failed because signs of log-ratio differences

were not the same and too few males were studied. In addition, we describe trees used for foraging, territorial singing, day-roosting, and resting.

The evaluation of habitat use requires sample periods that are long enough to allow an animal to visit available habitats and enough time between successive locations for the animal to depart a habitat. That is, successive locations should be independent (Swihart et al. 1988). We examined independence among an owl's successive foraging locations with Schoener's t^2/r^2 ratio (where t = time between locations and r = variance; Schoener 1981, Swihart and Slade 1985).

Finally, because foraging locations of Flammulated Owls tended to be aggregated, we used a cluster analysis (Ball and Hall 1967) to help quantify and delineate areas used repeatedly. We gridded (10 m × 10 m) the study area on the aerial photographs of plotted locations and referenced foraging locations to their nearest grid corners. The cluster program ISODATA, which locates nearest neighbors (Euclidian distance) by progressively subdividing a single large cluster (all home ranges in a year) into smaller clusters, was used in separate runs for the 1982 and 1983 foraging locations. For each prospective cluster, we ceased iterations when the next iteration subdivided the cluster that was obvious on aerial photos and on the ground. The within-cluster mean squared errors at this iteration ranged from 3.4 to 26.7 ($\bar{x}$ = 14.9 ± 7.0 SD) for 15 clusters in seven home ranges. Because we defined repeated foraging as six or more locations, clusters identified in the final iteration that had fewer than six foraging locations were rejected. We delineated clusters with the MCP method and measured areas with a planimeter; we refer to these areas as intensive foraging areas (IFAs). We calculated distances from IFAs to respective nests from IFA centroids.

RESULTS

The effects of radio-transmitters on Flammulated Owls appeared to be negligible. Owls returned to normal activity within 30 min of release and there was no evidence that nesting was impaired. For example, 5 broods (excluding 2 nests where brood size could not be determined) whose adult males were radio-tagged had a mean 2.6 ± 0.6 nestlings of bandable age, whereas 59 broods whose adult males were not radio-tagged (same study area, 1981–1997) had a mean 2.1 ± 1.0 nestlings (Linkhart and Reynolds, unpubl. data).

Home range.—While some home ranges shared common boundaries, especially along ridgetops, there was little overlap of MCP home ranges (Fig. 1). In the single case where the same male's home range was determined in both years (A29), the shapes of the home ranges differed because the male used different areas for resting (same nest used in both years; Fig. 1). Excluding extra-range movements (16 cases; Reynolds and Linkhart 1990), the maximum distance we observed any owl from its nest was 636 m (A11-83, foraging).

We recorded fewer total locations for males in 1982 ($\bar{x}$ = 50 ± 7 locations/home range) than in 1983 ($\bar{x}$ = 85 ± 18 locations/home range) as a result of differences in the timing and focus of sampling between years and seasonal changes in male behavior (Table 1). We monitored singing males a total of 10 h (54%) less in the period prior to egg-hatching in 1982 than in 1983. Because of this, and because breeding males sang more frequently prior to egg-hatching (Reynolds and Linkhart 1987), we recorded fewer territorial song locations per home range in 1982 (excepting A11-83; Table 1). We also recorded fewer day-roosting locations per home range in 1982 because telemetry began 9 days later (5 days prior to egg-hatching) in this year, and only radio-tagged males could be located on day roosts. Number of foraging and resting locations per home range changed little between years because most were determined after egg-hatching, a period similarly sampled in both years.

Measured home range sizes (Table 2) were significantly smaller in 1982 ($\bar{x}$ = 11.1 ± 1.9 ha) than in 1983 ($\bar{x}$ = 18.3 ± 5.1 ha; t = 2.65, df = 5, P = 0.04), probably because of less sampling effort in 1982. Proximity of some territorial song locations to home range boundaries, especially in 1983 (Fig. 1), suggests that Flammulated Owls defended type A territories (Hinde 1956).

Second-order habitat selection.—Of the five overstory types on the study area, old ponderosa pine/Douglas-fir was the most common (58% of total area), followed by young Douglas-fir/blue spruce (27%), mature quaking aspen/blue spruce (11%), mature quaking aspen (3%), and meadow (1%) (Table 2, Fig. 1).

Nests in five of the seven home ranges (A15-82, A24-82, A29-82, A4-83, and A29-83) were on the south facing slope of a main ridge in the study area. Overstories within these five home ranges were primarily old ponderosa pine/Douglas-fir ($\bar{x}$ = 84 ± 7% of home ranges, range = 74–92%; Table 2, Fig. 1). Nests in two home ranges (A10-82 and

TABLE 2. Overstory composition of study area (452 ha) and home ranges of Flammulated Owls in Colorado, 1982–1983.

	Home range size ha	Old[a] ponderosa pine/Douglas fir		Young[b] Douglas-fir/ blue spruce		Mature[c] quaking aspen/ blue spruce		Mature[d] quaking aspen		Meadow	
		ha	%	ha	%	ha	%	ha	%	ha	%
Study Area		264	58	122	27	47	11	14	3	5	1
A10-82	8.5	6.2	73	0.4	5	1.9	22	—	—	—	—
A15-82	11.0	9.8	89	1.2	11	—	—	—	—	—	—
A24-82	12.5	10.1	81	0.1	1	0.8	6	1.5	12	—	—
A29-82	12.5	10.7	85	1.2	10	—	—	0.6	5	—	—
A4-83	14.0	12.9	92	—	—	—	—	1.1	8	—	—
A11-83	24.0	13.2	55	3.5	14	5.0	21	2.3	10	—	—
A29-83	17.0	12.5	74	1.2	7	1.3	8	1.3	7	0.7	4
$\bar{x}$ within home ranges	14.2	10.8	78	1.1	7	1.3	8	1.0	6	0.1	<1
SD within home ranges	5.0	2.4	13	1.2	5	1.8	10	0.8	5	0.3	2

[a] 200–400 years.
[b] <100 years.
[c] 100–200 years.
[d] 75–125 years.

A11-83) were in creek bottoms in mature quaking aspen/blue spruce. The home ranges of the latter males were comprised of 73% and 55% old ponderosa pine/Douglas-fir, respectively. Compared to the proportion of each overstory type within the study area (Table 2), the seven home ranges contained a mean 20% (95% confidence interval ± 12%) more old ponderosa pine/Douglas-fir, 20% (±5%) less young Douglas-fir/blue spruce, and similar amounts of mature quaking aspen/blue spruce (8 ± 9%), mature quaking aspen (5 ± 4%), and meadow (1 ± 1%).

Third-order habitat selection.—Males were the principal food providers at nests throughout the breeding season, including the period after egg-hatching when rates of prey delivery to nests were highest. Females foraged little from early courtship until several nights before the young fledged (Reynolds and Linkhart 1987). Foraging males gleaned insects (mostly lepidopterans) from the needles, limbs, and trunks of large conifers, and occasionally hawked flying insects between tree crowns or dropped from the lower crown branches to capture arthropods on the ground (Reynolds and Linkhart 1987).

Flammulated Owls are single-prey loaders, delivering one prey item per trip to nests (Reynolds and Linkhart 1987). Single-prey loading requires males to make successive decisions to either return to where they previously foraged or to enter new areas following each prey delivery. Autocorrelation (t^2/r^2 ratios) among successive foraging locations of the seven radio-tagged males ranged from 0.55–1.97. Only one male (A29-83) exceeded the critical value (ratio = 1.97, critical value = 1.51); thus, with the exception of this male, successive foraging locations of males were autocorrelated. The autocorrelation in our sample reflected the tendency of owls to revisit favored foraging areas (see below). For Flammulated Owls the time to independence (Swihart and Slade 1985) was the elapsed time between a prey capture (and subsequent delivery of prey to the nest) and the next foraging attempt. Depending on the stage of nesting and time of night, the time between successive prey deliveries at nests varied from 1–60 min (Reynolds and Linkhart 1987). We used all foraging locations rather than an independent subset (see Swihart et al. 1988) in the preference analysis of foraging habitat because foraging locations were behaviorally independent.

Preference analyses (males combined, n = 7) of four overstory types used for foraging ("meadow" not included because of its negligible area) indicated that use of types differed significantly from availability (χ^2 = 18.70, df = 3, P = 0.001; Table 3, Fig. 2).

TABLE 3. Use and availability of four overstory types within seven home ranges by foraging male Flammulated Owls in Colorado, 1982–1983.

Overstory type	Total area (ha) in home ranges	Expected[a] proportion of locations	Expected[b] number of locations	Observed proportion of locations	Observed number of locations	Bonferroni confidence interval on proportion of occurrence
Old ponderosa pine/Douglas-fir	75.4	0.76	169	0.86	190	$0.799 \leq P_1 \leq 0.921$*
Young Douglas-fir/blue spruce	7.6	0.08	17	0.00	1	$-0.009 \leq P_2 \leq 0.017$*
Mature quaking aspen/blue spruce	9.0	0.09	20	0.10	23	$0.050 \leq P_3 \leq 0.158$
Mature quaking aspen	6.8	0.07	15	0.03	7	$0.001 \leq P_4 \leq 0.604$*
Total	98.8	1.00	221	0.99	221	

[a] Proportion of each overstory type available within the home ranges.
[b] Calculated by multiplying the expected proportion and the total number of locations (e.g., 0.76 × 221 = 169).

Bonferroni simultaneous confidence intervals indicated that old ponderosa pine/Douglas-fir was significantly over-selected while young Douglas-fir/blue spruce and mature quaking aspen overstories were significantly under-selected. Mature quaking aspen/blue spruce was used in about the same proportion as available.

Intensive foraging areas.—A mean 81 ± 8% (range = 71–93%, n = 7 males) of 221 total foraging locations occurred in 15 IFAs. Two home ranges contained one IFA, three ranges contained two IFAs, one contained three, and one range contained four (Fig. 1). There was a mean 12 ± 6 foraging locations (range = 6–25 locations) per IFA and each male was observed foraging in a particular IFA on two to four different nights. Mean size of IFAs was 0.5 ± 0.4 ha (range = 0.1–1.4 ha), and mean total area in IFAs per home range was 1.0 ± 0.3 ha (range = 0.6–1.5 ha). Mean distance of IFAs from nests was 126 ± 123 m (range = 10–401 m). Except for the A11-83 nest, each nest occurred within an IFA. When males foraged in nest IFAs or in IFAs nearest the nest, which occurred frequently in the early evening (20:00–21:30) and at infrequent intervals later in the night, prey delivery rate to nests was one prey every 1–10 min. Later in the night, the delivery rate fell to one every 10–20 min (Reynolds and Linkhart 1987); some males (A10-82, A15-82, and A29-82) foraged in IFAs farther from nests (>250 m) at this time. The two males whose ranges contained only a nest IFA (A4-83 and A29-82) foraged in the nest IFA regardless of the time of night. The nest IFA of A29 (same male in both years) was nearly identical in location and shape in both years. However, in 1983 this male also foraged in a new IFA on the edge of his home range. Twelve of the 15 IFAs (80%) consisted entirely of old ponderosa pine/Douglas-fir, two (13%; one each in A10-82 and A11-83) con-

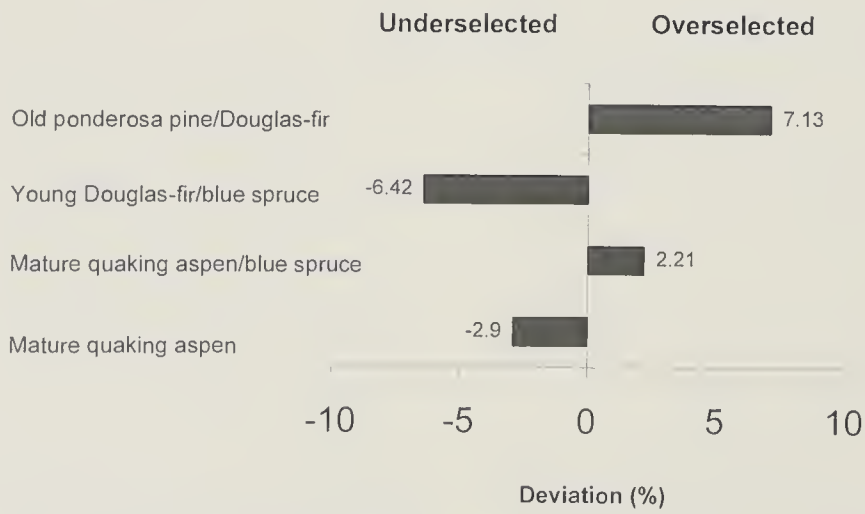

FIG. 2. Percent deviation (Neu et al. 1974) from expected use of four overstory types by foraging Flammulated Owls.

TABLE 4. Percent of telemetry locations by tree species and the percentages of trees available on the study area in Colorado, 1982–1983.

Tree species	Percent of trees available (615)[a]	Activity			
		Foraging (167)[b]	Territorial singing (22)[b]	Day-roosting (112)[b]	Resting (19)[b]
Douglas-fir	39	61	50	58	58
Ponderosa pine	29	19	50	26	35
Quaking aspen	17	9	—	1	1
Limber pine[c]	10	6	—	9	6
Blue spruce	5	5	—	6	—
Total	100	100	100	100	100

[a] Number of trees randomly sampled across study area.
[b] Total number of trees.
[c] *Pinus flexilis.*

sisted entirely of mature quaking aspen/blue spruce, and one (7%; A11-83) consisted of old ponderosa pine/Douglas-fir mixed with quaking aspen.

Foraging trees.—Of 167 trees in which a prey was known to have been captured (excluding cases of hawking, ground foraging, and uncertain sites of capture), 61% were Douglas-fir and 19% were ponderosa pine (Table 4). Mean age of 77 trees randomly selected from these foraging trees was 199 ± 85 years (range = 72–395 years).

Song trees.—Males sang from one to eight trees during an episode of territorial song, and song trees were mostly on mid-slopes and ridgetops. Males frequently sang from within the lower tree crown next to the trunk. Mean age of 22 song trees (exact tree unknown in 76 cases) was 289 ± 96 years (range = 94–419 years); 50% were Douglas-fir and 50% were ponderosa pine (Table 4).

Day-roost trees.—Of 112 day-roost trees of males, 58% were Douglas-fir and 26% were ponderosa pine (Table 4). Perches used by males in day-roost trees typically had a dense, overhead cover of horizontal limbs and/or foliage. During the nesting season males repeatedly roosted in selected trees; 19% of roost trees were used 2–20 times, and these trees accounted for 75% of all day-roost trees. Mean age of day-roost trees was 207 ± 106 years (range = 88–508 years, n = 55). Mean distance between male day-roosts and nest trees was 90 ± 58 m (range = 10–255 m, n = 112 roosts). However, all males day-roosted within 20 m of their nests during the four days before fledging (Linkhart 1984).

Resting trees.—At night, males occasionally rested or perched quietly up to one hour in trees at scattered locations in their ranges. Before eggs hatched males rested occasionally at any hour of night, while after eggs hatched males rested occasionally in the late evening after broods had been fed. During rainy periods, males ceased foraging and rested in protected areas in large trees with dense crowns. The majority of resting trees were Douglas-fir (58%) and ponderosa pine (35%) (Table 4).

DISCUSSION

Radio-telemetry showed that Flammulated Owls established home ranges in areas that contained more old ponderosa pine/Douglas-fir than other overstory types available within the study area. Males also foraged most often in old ponderosa pine/Douglas-fir, and most intensive foraging areas (IFAs) consisted entirely of this overstory type. Most nests of Flammulated Owls were within an IFA, which probably resulted from the owls' need to minimize travel time between nests and foraging sites during periods of high feeding rates. After eggs hatched, males foraged for their broods in the vicinity of nests in the early evening, making as many as 16 trips per hour to nests (Reynolds and Linkhart 1987). Reducing travel time is important because only one small (<0.3 g) prey is delivered per trip (Reynolds and Linkhart 1987). Thus, use of microhabitats depends on their availability and juxtaposition, both of which are affected by choices of habitats made at higher orders of selection.

Male Flammulated Owls used Douglas-fir trees more often than ponderosa pine for foraging, day-roosting, and resting. Old Douglas-fir trees typically appeared to have greater crown volume than old ponderosa pine trees, providing more crown and trunk surface area for foraging, and greater cover for day-roosting and resting. In Idaho (Powers et al. 1996) and southern British Columbia (Howie and Ritcey 1987), Flammulated Owls nested in Douglas-fir forests where little or no ponderosa pine was present.

The use of older stands of ponderosa pine/Douglas-fir by Flammulated Owls on our study area is probably related to habitat struc-

ture and prey availability. Older forests typically contain an abundance of snags and lightning-damaged trees with cavities (Reynolds et al. 1985), and Flammulated Owls may have a higher probability of finding nest cavities there. Second, open stands of large, old ponderosa pine/Douglas-fir forest with grass or shrub understories suit the foraging behaviors used by Flammulated Owls within and between crowns, on crown surfaces, and in understories (Reynolds and Linkhart 1987). Third, ponderosa pine and Douglas-fir trees contain up to four times as many lepidopteran species as other western conifers (Furniss and Carolin 1977). Lepidopterans are important prey of Flammulated Owls during the breeding season (Reynolds and Linkhart 1987, Powers et al. 1996). Finally, ponderosa pine/Douglas-fir forests contain an abundance of the large, old trees used by Flammulated Owls for foraging, territorial singing, and day-roosting.

The importance of old ponderosa pine/Douglas-fir to the owl is underscored by data on occupancy and habitat composition of territories on the study area from 1981–1996. Occupancy of territories by breeding pairs was positively correlated with the amount of old ponderosa pine/Douglas-fir, and negatively correlated with the amount of young Douglas-fir/blue spruce, in 14 ha circles centered in territories (Linkhart and Reynolds 1997). Territories most often occupied by unpaired males contained relatively small percentages of old ponderosa pine/Douglas-fir in 14 ha circles (Linkhart and Reynolds 1997).

The structure and species composition of old ponderosa pine/Douglas-fir forests used by Flammulated Owls were historically maintained by frequent, low-intensity ground fires (Cooper 1960). Fire suppression has resulted in increased tree densities in ponderosa pine and mixed-conifer forests, has converted many pine forests to fir forests, and has changed fire type from low-intensity to catastrophic, habitat-destroying, crown fire (Barrett et al. 1980, Gordon 1980). In addition, many old ponderosa pine and mixed-conifer forests within the range of the Flammulated Owl have been harvested. These habitat changes have resulted in declines of Flammulated Owls in some areas (Marshall 1957, 1988; Phillips et al. 1964; Franzreb and Ohmart 1978). Forest management prescriptions that restore the species composition and structure of these forests are needed.

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VOCALIZATIONS OF THE BLUE-FRONTED AMAZON (*AMAZONA AESTIVA*) IN THE CHANCANÍ RESERVE, CÓRDOBA, ARGENTINA

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ABSTRACT.—The calls of the Blue-fronted Amazon (*Amazona aestiva*) are described and their possible function within the social organization of the species during breeding and non-breeding seasons are discussed. We identified 9 vocalizations; six ("wak-wak", "wa-wawawa", transitions, "gu-gugu", guturals, "ka-kaka") were nonspecific and were given in several circumstances: alarm, contact, feeding, and flying. The remaining had specific contexts: "waahh" (agonistic), "grr-uíp" (contact in flight), and songs (reproduction-territorial). Vocalization rates increased in alarm contexts and during the non-breeding season, probably as a result of increasing interactions between individuals. The frequency containing the greatest amount of energy was a useful variable to characterize Blue-fronted Amazon calls, particularly at the species level. The most commonly used vocalization, "wak-wak", has structural features that promote directionality and short-range transmission, enhancing its usefulness for the aggregation of individuals. It is suggested that songs were derived from a process of repetition and increasing variability from gutural calls. The highly contextual variability of these calls may be due to an incompletely specialized repertoire or a vocal system based upon combinations of calls for conveying messages. *Received 5 May 1997, accepted 17 Mar. 1998.*

The Blue-fronted Amazon (*Amazona aestiva*) is a parrot whose distribution extends over northeastern Brazil, Bolivia, Paraguay, and northern Argentina (Forshaw 1977, Darrieu 1983). Populations have declined in recent years, especially as a result of habitat destruction and over exploitation by pet trade (Bucher and Martella 1988, Bucher et al. 1992, Beissinger and Bucher 1992, Nores and Yzurieta 1994). This species is locally extinct in certain areas of southern Argentina; nevertheless, small populations survive in some isolated forest patches, such as in the Chancaní Reserve, province of Córdoba (Bucher et al. 1992, Fernández-Juricic et al. 1998).

Blue-fronted Amazons feed on fruits and seed and they can attack crops, especially citrus (Forshaw 1977, Navarro et al. 1991, Sauad et al. 1991a). During the non-breeding season, flocks fly from roost sites in the morning to feeding areas, returning in the afternoon (Forshaw 1977, Sauad et al. 1991b, Mosa et al. 1992). In the breeding season (September–March), isolated pairs nest in cavities of mature trees such as the quebracho blanco (*Aspidosperma quebracho-blanco*) and the palo blanco (*Calycophyllum multiflorum*; Bucher and Martella 1988, Nuñez et al. 1991). Because these cryptically colored parrots spend most of their time in tree canopies, their presence is generally detected only by their loud vocalizations. Although Vielliard (1994, 1995) analyzed some vocalizations of the Blue-fronted Amazon for phylogenetic comparisons, the vocal repertoire of this species has not been studied comprehensively.

The objectives of this work were to identify the vocalizations of the Blue-fronted Amazon and analyze their functions within the social organization of this species.

METHODS

The study was carried out in the Natural Provincial Park and Natural Reserve of Chancaní, Córdoba, Argentina (6° 26′ W; 30° 22′ S), which encompasses 4920 ha of undisturbed Chaco forest and where the dominant plant community is the quebracho-blanco forest. Annual precipitation ranges from 300–550 mm (Capitanelli 1979).

We visited the reserve during breeding and non-breeding seasons (December 1993, March, May, August and October 1994), accumulating 100 sampling hours. In each visit, we first determined the areas within the reserve where the parrots were most actively seen or heard to concentrate our sampling efforts. We recorded vocalizations during the morning (from 30 minutes before sunrise to mid-morning) and in the af-

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ternoon (3 hours before sunset until sunset). Behavioral observations were accomplished according to focal sampling techniques (Altmann 1974). Sexes were not distinguishable because the Blue-fronted Amazon is sexually monomorphic.

Vocalizations were recorded with an UHER 4000IC tape recorder at a speed of 19.05 cm/s and a directional microphone (Electro-Voice Model 644). We used a 16-bit stereo Sound Blaster advanced signal processor to digitize sounds at sampling rates up to 22.05 kHz to exceed Nyquist frequency (two times the upper frequency of sampled vocalizations; Evans and Evans 1994, Wilkinson 1994). Signals were filtered at the Centro de Investigaciones Acústicas y Luminotécnicas (C.I.A.L., Córdoba), removing low frequencies (<500 Hz). Sonograms were made at the Instituto de Medicina y Biología Experimental (IBYME, Buenos Aires) with the software ADDA 16 (Laboratorio de Investigaciones Sensoriales 1992). To standardize and facilitate comparisons, sonograms were displayed with an arbitrary scale of 2.5 s and two frequency scales: 0–10 kHz and 0–11.03 kHz.

We adopted the following terms to describe the calls (Kreutzer 1983, Martella 1985): note, a short sound not interrupted by a silence; syllable, a group of several different notes; and complex syllable, a group of different notes that constitute a coherent unit in the sonogram. The frequency band where most of the acoustic energy was concentrated was designated as energy concentration. Multiples of the fundamental were called harmonics. Based upon the onomatopoeias of the calls, we named each sound avoiding interpretive terms and/or discreet categories (fight calls, for instance) that might have implied some motivation of the individuals to behave in a certain way (Stirling and Roux 1987, Miller 1992).

We first performed a structural analysis to identify units and then we related them to the contexts in which vocalizations were uttered. Structurally, we measured the following variables: low frequency (the lowest frequency record, in Hz), high frequency (the highest frequency record, in Hz), frequency range (the difference between the latter variables, in Hz), energy concentration (as described above, in Hz), and duration (in ms). For each one of these variables, we calculated: mean, standard deviation (SD) and coefficient of variation (CV). The latter variability measure proved to be useful for detecting trends in individual and species recognition (Catchpole 1979, Saunders 1983, Sparling 1983). Temporal and morphological methods (see Thompson et al. 1994 for details) allowed us to classify songs, taking into account the time intervals among notes and the repetition of notes forming clear patterns.

Vocal activity (vocalization rate) was estimated as the number of notes per s in different contexts—alarm, flying, perching. Kruskal-Wallis and Mann-Whitney tests were performed to assess statistical differences among vocalization rates and among note intervals of songs. All analyses were performed using Statistica (version 4.5).

RESULTS

We identified nine vocalizations; six ("wak-wak", "wa-wawawa", transitions, "gu-gugu", guturals, "ka-kaka") were nonspecific and were uttered in several circumstances: alarm, contact, feeding, flying. The remaining three were given in specific contexts: "waahh" (agonistic), "grr-uíp" (contact in flight) and songs (reproduction-territorial).

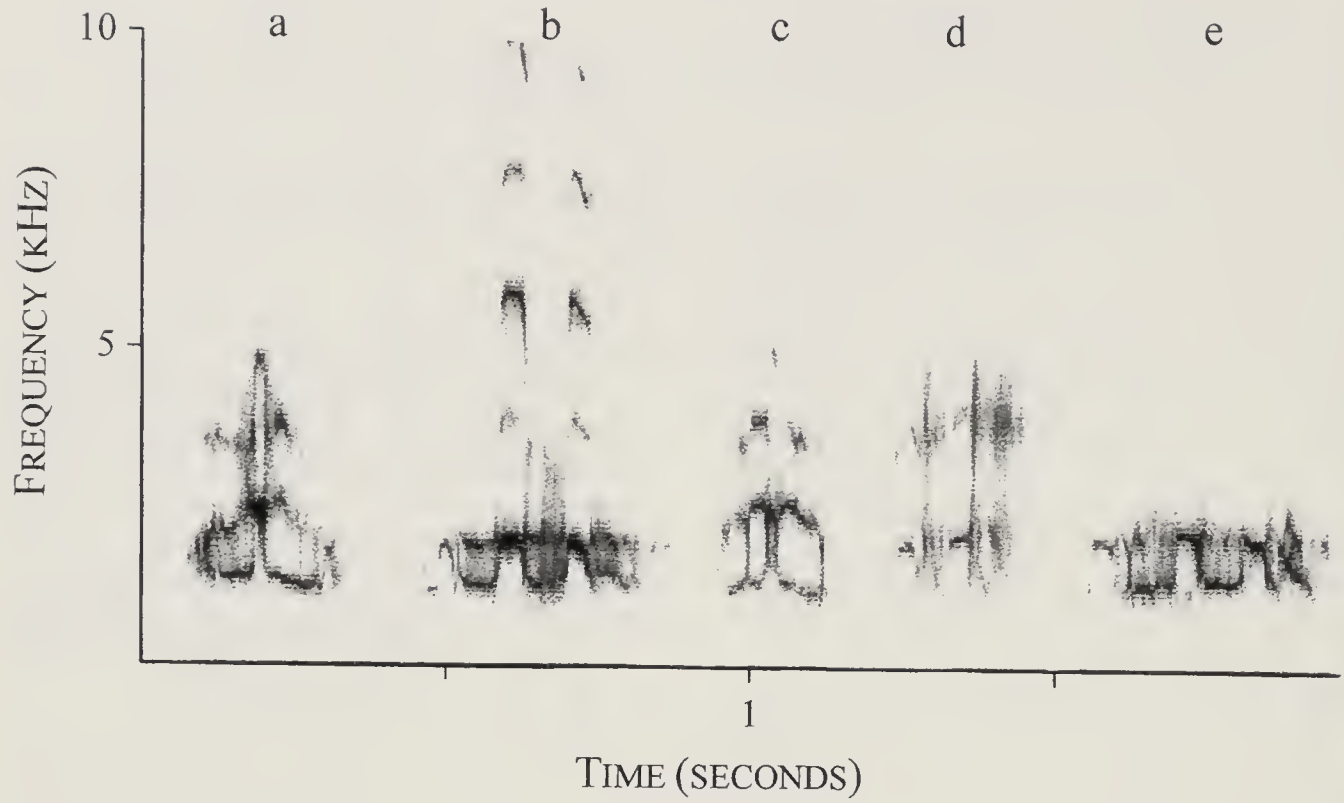
"*Wak-wak*".—This is the typical vocalization of the Blue-fronted Amazon uttered all year round. It has a wide frequency range (approximately 1000–5700 Hz) with a central axis and lateral branches (Fig. 1a, Table 1). We were able to identify individuals based on differences in vocalization such as inflections in the lower bands, extra bands at 7500 or 10,000 Hz, and additional segments.

Wak-waks were given in series but without a constant temporal pattern. This vocalization was used during flight (alone or in groups), takeoff and landing, in stress situations provoking alarm (the presence of intruders), and when parrots communicated at long and short distances. Typical alarm responses (flying away uttering wak-waks) changed during the breeding season: breeding pairs remained perched giving wak-waks and then flew away quietly from intruders.

"*Wa-wawawa*".—This vocalization was given year round, but less frequently than wak-wak, and in alternation with other calls. The fundamental warbles in frequency and has harmonics associated with it, producing a wide frequency call, while note duration is much longer than wak-waks (Fig. 1b, Table 1).

Wa-wawawa was uttered in several contexts: usually flying (alone or in a group), perching, in vocal contacts with other parrots, and during landings in response to conspecific calls. This note might have a contact function, because of its association with coordinated movements and position changes during flights.

Transitions.—These vocalizations were heard during nearly all of the study period. We distinguished two types: transition toward wak-wak (more frequent; Fig. 1c) and transition toward wa-wawawa (Fig. 1d). Transitions look like incomplete wak-waks or wa-wawawas, respectively, indicating that they keep



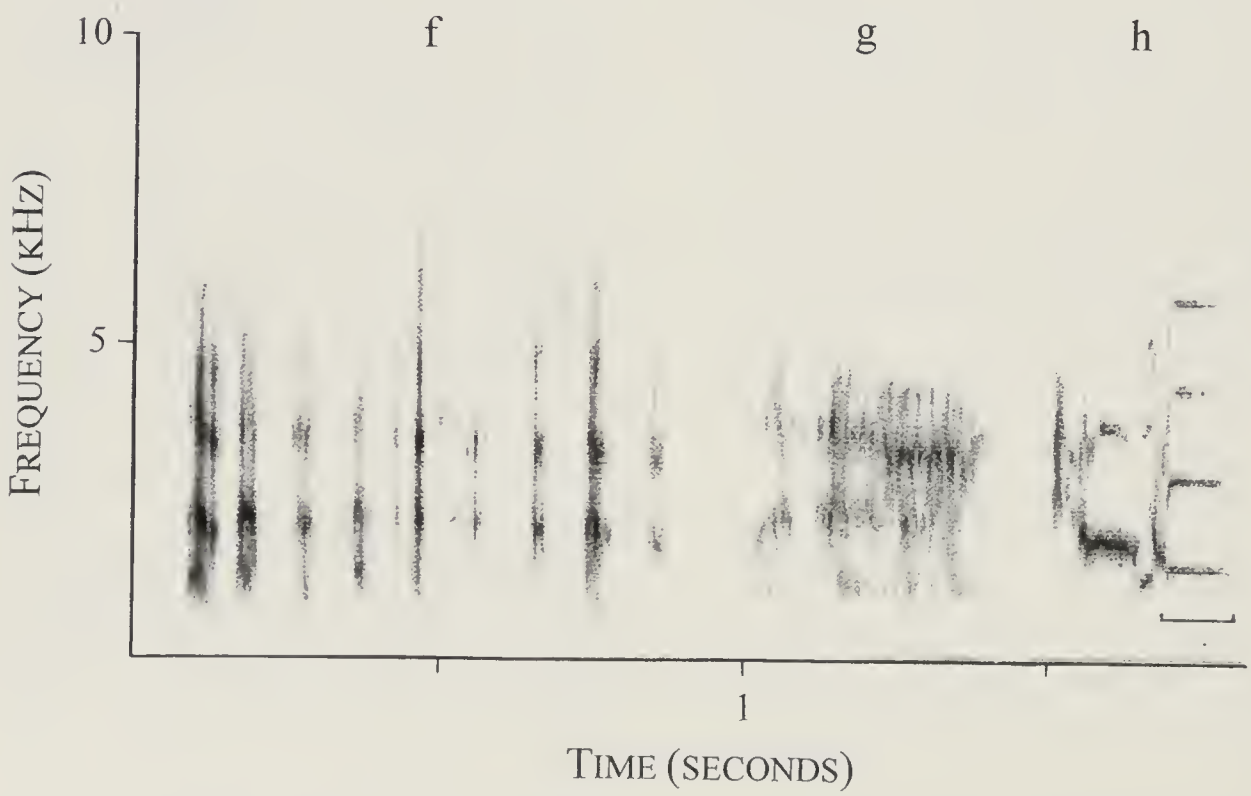


FIG. 1. Blue-fronted Amazon vocalizations indentified in the Chancaní Reserve, Córdoba, Argentina (and the usual contexts in which they were observed): (a) "wak-wak" (the call most frequently used in several situations), (b) "wa-wawawa" (coordination of position changes during flight), (c) transition to "wak-wak" (alarm), (d) transition to "wa-wawawa" (prior to the emission of "wak-waks"), (e) "gu-gugu" (contacts of flying and perching parrots), (f) "kakaka" (feeding), (g) "waahh" (agonistic situations), (h) "grr-uíp" (contact in flight; the most common syllable is indicated).

TABLE 1. Structural characteristics of "WAK-WAK," "WA-WAWAWA," transition to "WAK-WAK," transition to "WA-WAWAWA," "GU-GUGU," "KA-KAKA," "WAAHH" and gutural calls of the Blue-fronted Amazon in the Chancaní Reserve, Córdoba, Argentina.

Vocalization (sample size)	Low freq. (Hz)	High freq. (Hz)	Freq. range (Hz)	Energy concn. (Hz)	Duration (ms)
"WAK-WAK" (n = 30)					
Mean	920.60	5706.90	4802.50	2402.80	243.20
SD	179.20	511.31	565.91	84.20	50.76
CV	19.47	8.96	11.78	3.50	20.87
"WA-WAWAWA" (n = 20)					
Mean	1005	5808.50	4805.30	2190.40	353.95
SD	166.33	764.12	725.31	272.01	79.078
CV	16.55	13.16	15.09	12.42	22.34
Transition to "WAK-WAK" (n = 9)					
Mean	1141.40	4854.80	3635.9	2373.40	147.44
SD	87.42	791.50	911.35	126.04	49.02
CV	7.66	16.30	25.07	5.31	33.25
Transition to "WA-WAWAWA" (n = 3)					
Mean	1008.3	5857	4884	2237.70	232.33
SD	123.27	823.18	847.48	56	2.31
CV	12.23	14.06	17.35	2.50	6.99
"GU-GUGU" (n = 12)					
Mean	1077.90	2474.40	1405.2	2056.80	253.17
SD	108.65	232.49	210.01	126.71	84.10
CV	10.08	9.40	14.95	6.16	33.22
"KAKAKA" (n = 62)					
Mean	247.32	5555.60	5308.30	3566	43.60
SD	228.28	795.48	889.21	219.52	8.09
CV	92.30	14.319	16.75	6.16	18.56
"WAAHH" (n = 15)					
Mean	492.67	7000.10	6507.50	2492.50	247.13
SD	243.87	1473.60	1550.80	197.92	170.86
CV	49.50	21.05	23.83	7.9409	8.27
Guturals (n = 76)					
Mean	860.49	3968.30	3068.40	1855.80	127.58
SD	330.01	1402.50	1649	429.39	50.16
CV	38.35	35.34	53.74	23.138	39.32

Abbreviations: Freq. = frequency; Conc. = concentration; SD = standard deviation; CV = coefficient of variation; Hz = Hertz; ms = milliseconds.

their basic shape, but are shorter and lack 1 or 2 of the characteristic frequency bands (usually the lower and the upper; Table 1). Transitions were recorded sporadically before wak-waks or wa-wawawas, when perching flocks vocalized repeatedly, and in alarm situations involving pairs.

"*Gu-gugu*".—This note was recorded at the end of the breeding season (March) and during the non-breeding season (May). It is a

TABLE 2. Physical characteristics of the most common sector of "GRR-UÍP" calls of the Blue-fronted Amazon in the Chancaní Reserve, Córdoba, Argentina.

(n = 7)	Low freq. (Hz)	High freq. (Hz)	Freq. range (Hz)	Energy conc. (Hz)	Harm. 2 (Hz)	Harm. 3 (Hz)	Harm. 4 (Hz)	Duration (ms)
Mean	1148	6229.90	5081.90	1481.90	2869	4392	5758.50	122.86
SD	164	648.85	664.21	68.72	255.78	247.84	225.69	18.83
CV	14.29	10.42	13.07	4.64	8.92	5.64	3.92	15.33

Abbreviations: Freq. = frequency; Conc. = concentration; SD = standard deviation; CV = coefficient of variation; Hz = Hertz; ms = milliseconds; Harm. = harmonics.

low pitched warble with variable duration. Energy is concentrated at the peak of the warbles (approximately 2000 Hz; Fig. 1e, Table 1). This call was heard when a large number of individuals (generally more than four) were flying and during vocal contacts between perching individuals. Sometimes, gu-gugus and wa-wawawas were associated in a long series.

"*Ka-kaka*".—It was given only during the non-breeding season. Structurally, it is formed by a series of an average of 15 notes (±4.73 SD), each with a wide frequency range (5300 Hz) and short duration (about 45 ms), separated by 50 ms intervals (Fig. 1f, Table 1). Kakakas were heard in foraging contexts (parrots in the canopy of quebracho blancos moving through branches, eating sprouts) and when large flocks were displaying continuous vocal activities in dense forests.

"*Waahh*".—This vocalization was uttered during March and August; however, for its analysis we used recordings taken at the Zoological Garden of Córdoba (Argentina) in order to obtain better sound quality. Waahhs are typically harsh sounding and have a wide bandwidth. Energy is concentrated at two frequency bands: 2500 and 3800 Hz (Fig. 1g, Table 1). The call was given in threat and fight contexts among conspecifics. When several parrots (>10) were in trees, some aggressive interactions took place. Usually one parrot moved its head toward another individual behind it, displayed its wings, and vocalized a single waahh. If the approach continued, the other parrot left or began fighting. As individuals came closer, call intensity and duration increased.

"*Grr-uíp*".—This call was given in March (post-breeding season) and in May (non-breeding season). It is a complex vocalization formed by two or three different syllables. The most common syllable spans nearly 120 ms and is distinguished by the presence of multiple harmonics. The average syllable has its greatest amplitude at 2100 Hz, lasting 390 ms (Fig. 1h, Table 2). Grr-uíp corresponded closely to flight movements which required certain coordination; for instance, when parrots changed their positions within flocks or when they displayed intricate maneuvers while landing in trees.

Gutural.—A very common vocalization throughout the year. Structurally, guturals are highly variable in their bandwidth, duration, and intensity (Fig. 2a, Table 1). They were associated with a variety of contexts: alarm, takeoff, flight, contact between members of a pair and among perching individuals. Moreover, they were given in series or combined with other vocalizations (particularly wak-wak, wa-wawawa and gu-gugu).

Songs.—They were recorded exclusively at the beginning of the breeding season (August). Structurally, songs constitute a series of different notes given in long succession and with a specific pattern. Based upon a sample from 1 individual and 6 complete songs, we identified 17 different notes, designated as Note 1 to 17. Physical characteristics and sonograms of the most common notes (Notes 1 to 6) are shown in Table 3 and Fig. 2b, respectively.

Songs are made up by two successive sets (Set 1 and 2). Set 1 is less variable than Set 2 and is formed by the sequence of Notes 4, 5, 6, and 1. Set 2 is more variable in relation to the type and number of notes (Notes 2, 3, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16 and 17). However, certain syntactic rules can be established: (1) Note 2 was the most frequently used, and generally alternated with the other notes in the following way: Nx_N2_Nx_N2_Nx. . .; where N2 is Note 2, Nx

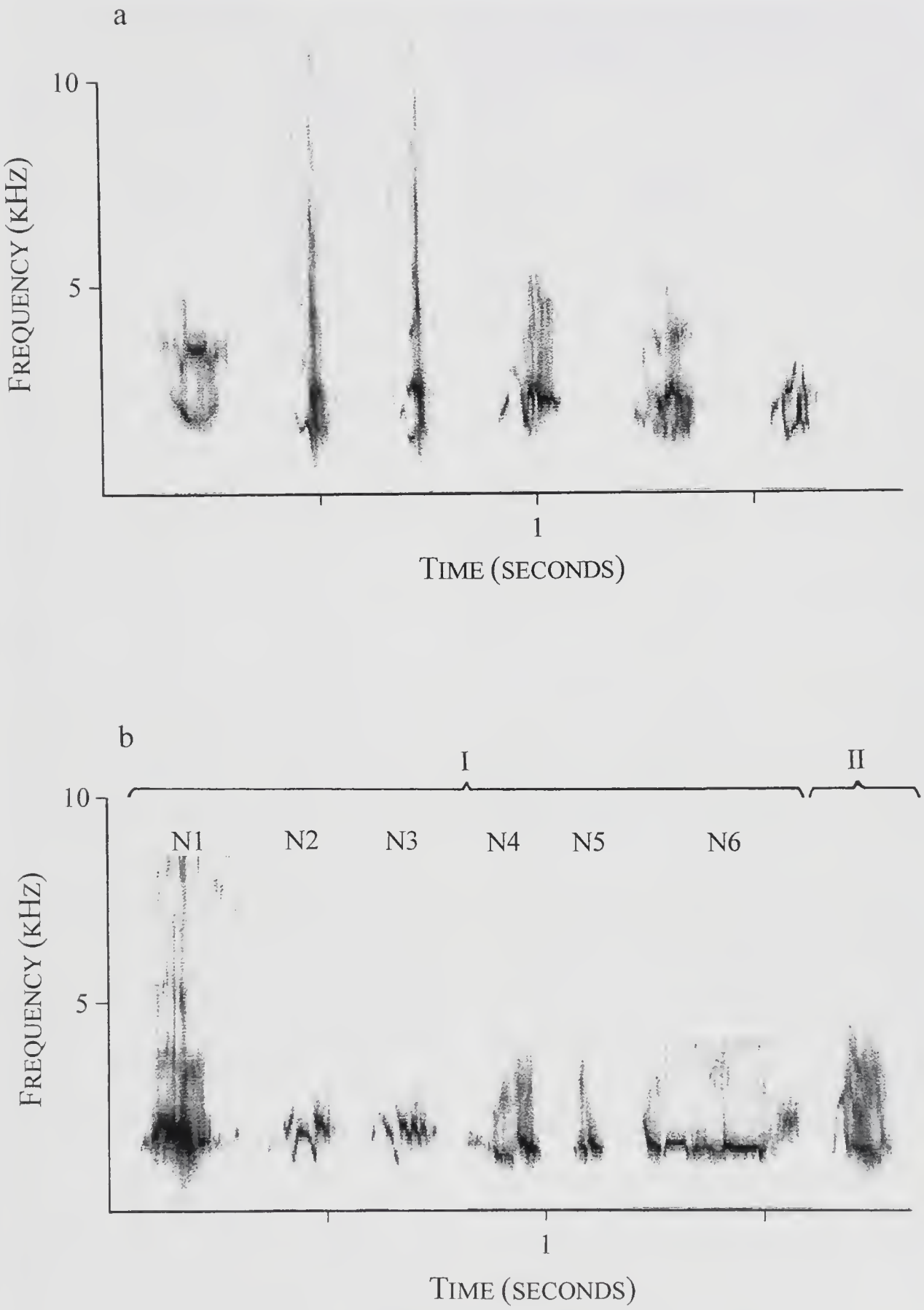


FIG. 2. Blue-fronted Amazon vocalizations recorded in the Chancaní Reserve, Córdoba, Argentina (and the usual contexts in which they were observed): (a) guturals (interaction between conspecifics), (b) songs (reproduction-territorial): I = notes commonly uttered, II = the only note vocalized by a hidden individual.

TABLE 3. Physical characteristics of the most common notes (Notes 1 to 6) of the songs of the Blue-fronted Amazon in the Chancaní Reserve, Córdoba, Argentina.

Note (sample size)	Low freq. (Hz)	High freq. (Hz)	Freq. range (Hz)	Energy conc. (Hz)	Duration (ms)
Note 1 (n = 6)					
Mean	409.67	10,390	9979	1951.80	274.17
SD	75.66	57.24	124.64	50.03	15.26
CV	18.468	0.5510	1.25	2.56	5.57
Note 2 (n = 7)					
Mean	869.67	2625.70	1756.10	1867.30	99.57
SD	121.32	88.44	171.17	99.69	10.74
CV	13.95	3.37	9.75	5.34	10.78
Note 3 (n = 7)					
Mean	943.43	2599.90	1665.40	1874.30	127.29
SD	97.42	321.59	405.58	85.76	62.69
CV	10.43	12.37	24.35	4.58	49.26
Note 4 (n = 6)					
Mean	931.17	3652.50	2721.30	1562.50	149.83
SD	62.46	461.42	424.47	93.54	18.78
CV	6.71	12.63	15.60	5.99	12.53
Note 5 (n = 5)					
Mean	1072	2552.40	1480.40	1511.80	68.40
SD	82.44	49.34	39.23	74.60	11.44
CV	7.69	1.93	2.65	4.93	16.72
Note 6 (n = 5)					
Mean	1044.60	2478.2	1433.6	1496.6	356.80
SD	45.50	113.79	122.43	18.84	4.02
CV	4.36	4.59	8.54	1.26	1.13

Abbreviations: Freq. = frequency; Conc. = concentration; SD = standard deviation; CV = coefficient of variation; Hz = Hertz; ms = milliseconds.

represents the remaining notes of Set 2 and _ is a time interval. The interval prior to Note 2 was significantly longer (302.64 ms ± 212.2 SD) than the subsequent interval (133.45 ± 26.8 SD; Mann-Whitney test: $U = -3.87$; $n = 22$; $P < 0.001$). (2) Note 3 was the second most commonly used note, and usually alternated with Note 2 (N3_N2_N3_N2_Nx . . ..). (3) We identified short Sets 2 ($\bar{x}$ = 3.25 notes; $n = 12$) and long Sets 2 ($\bar{x}$ = 10 notes; $n = 6$).

Two parrots were sampled for 5 days moving around a restricted sector of dense forest. When another pair approached within 500 m, both pairs began vocalizing songs. We focused our recordings on one pair in which the singer was perched on a conspicuous branch. Hidden within the canopy, the other member of the pair gave only one structurally different note (Fig. 2bII) at the end of each bout. Shortly before, both pairs were involved in a flying fight, vocalizing agonistic, gutural, and contact calls. It is probable that the intruders were trying to locate a suitable nesting site, which suggests a territorial context.

Vocalization rates.—Blue-fronted Amazons vocalized more frequently in alarm situations (2.25 notes/s) than in perching (1.24 notes/s) or flying contexts (1.42 notes/s) (Kruskal-Wallis test: $F_{2,57} = 10.54$; $P < 0.01$). Flying vocalization rates were not significantly different between sampled months (Kruskal-Wallis test: $F_{2,20} = 1.31$; $P > 0.05$). However, perching vocalization rates showed significant differences between March (1.03 notes/s), May (1.64 notes/s), August (1.42 notes/s) and October (0.73 notes/s; Kruskal-Wallis test: $F_{3,32} = 8.09$; $P < 0.05$). Perching vocalization rates were not significantly affected by our presence (1.2 notes/s) compared to vocalization rates of birds that did not detect us (1.3 notes/s; Mann-Whitney test: $U = 0.57$; $n = 26$; $P > 0.05$).

DISCUSSION

Blue-fronted Amazons' vocalizations have most of their acoustic energy concentrated in low frequencies, which may be adaptive, because these frequencies attenuate and degrade in forest habitats less than those of higher frequencies (Morton 1975). In addition, the concentration of energy is the structural feature showing the least variability (the lowest coefficients of variation), suggesting that it transmits information about species identity (Berger and Ligon 1977, Catchpole 1979, Saunders 1983, Sparling 1983). Conversely, note duration, with a higher coefficient of variation, could convey information about the identity of each individual (Berger and Ligon 1977, Catchpole 1979, Saunders 1983). Although the analysis of coefficients of variation does not constitute a definitive proof of the outlined distinctions, we suggest that species and individual identity certainly could be transmitted by means of acoustic structural variations.

Wak-wak, the most used call in alarm contexts, contains many structural features that would promote directionality and short-range information transmission: abrupt beginning and end, wide frequency range, frequency variations, and note repetition (Marler 1955, Catchpole 1979, Richards 1985). These properties would allow conspecifics to quickly locate each other and confer a selective advantage in contexts where contacts between individuals are necessary for group coordination (Thorpe 1961).

Gutural calls were used to maintain contact between flying or perching individuals. The contexts in which guturals, wa-wawawas and gu-gugus were uttered (mainly during the non-breeding season) would indicate the use of the three calls for the interaction and coordination of conspecifics. The chatter of the Monk Parakeet (*Myopsitta monachus*; Martella and Bucher 1990) and the gutural calls of the Blue-fronted Amazon are structurally similar: both constitute different figures separated by short intervals. Nevertheless, it is difficult to see a functional similarity because Monk Parakeets utter these calls in more restricted circumstances, such as when social groups are perching near or within nests. Similar vocalizations are found in other sociable species, including the Sociable Weaver (*Philetairus socius*; Channing and MacLean 1976) and the Piñon Jay (*Gymnorhinus cyanocephalus*; Berger and Ligon 1977). Blue-fronted Amazons' grr-uíps and Monk Parakeets' contact vocalizations (Martella and Bucher 1990) are complex syllables, divisible into two well distinguished sectors. Although the Monk Parakeet uses these complex vocalizations in a wide variety of situations, it shares with the Blue-fronted Amazon the fact of using them when flying parrots huddle together and when landing in trees with conspecifics.

Wide frequency range and the acoustic energy concentrated at low frequencies are two features that characterize whhaa calls. Similar vocalizations are uttered in the same sort of agonistic contexts by other psittacine species, namely Orange-chinned Parakeets (*Brotogeris jugularis*; Power 1966) and Short-billed White-tailed Black Cockatoos (*Calyptorhynchus funereus latirostris*; Saunders 1974, 1983).

Parrot songs also have been observed in some Australian species, such as *Psephotus haematonotus* (Forshaw 1977), and *Melopsittacus undulatus* (Farabaugh et al. 1992). Apparently, Blue-fronted Amazons' songs have a territorial function. It is thought that this species is monogamous and keeps its pair-bonds throughout life; therefore, there would be little need for mate attraction. Instead, defending a territory that provides a critical resource (such as nest trees) turns out to be more relevant to ensure reproductive success. Furthermore, these vocalizations might also serve other subtle functions: synchronization of reproductive periods in the pair, stimulation of females to a proper physiological state for reproduction, and maintenance of pair-bonds (Catchpole 1979, McGregor 1991, Farabaugh et al. 1992).

Songs have narrow bandwidths, no harmonics, and energy concentrated at low frequencies; features allowing long distance transmission of signals in forests (Morton 1975, Wiley and Richards 1982, Richards 1985). We suggest that Blue-fronted Amazon songs evolved from a process of repetition and increased variability. The original vocalizations could have been gutural calls which structurally resemble the notes of the songs. Many bird species, including songbirds (*Parus sclateri*;

Ficken 1990), and parrots (*Melopsittacus undulatus*; Farabaugh et al. 1992), incorporate calls in their songs, a hint of this process.

We found that vocalization rates increased when individuals were alarmed. Differences in the rates of vocalization by perching parrots might imply activity variations throughout the year. May's highest value (non-breeding season) would be the result of a higher rate of interactions, since parrots spent more time together—flying in large flocks, feeding in groups and sharing communal roost sites (Fernández-Juricic 1994). The second highest value was in August, a transition period between breeding and non-breeding seasons (Fernández-Juricic et al. 1998). October and March had the lowest rates because activities are reduced to the interaction of the pair and their juveniles during the breeding season.

Only three of nine vocalizations could be associated with specific contexts; the other calls were given in a variety of situations, a fact that partially corroborates the vocal flexibility of this species in captivity (Forshaw 1977). On the whole, the high contextual variability found in the Blue-fronted Amazon calls may be partially accounted for by two possibilities: an incompletely specialized vocal repertoire (with high degrees of redundancy) or a vocal repertoire in which combinations of calls convey different messages. Neither of these prospects can be assessed with the available data and both need further testing.

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PILEATED WOODPECKER DAMAGE TO RED-COCKADED WOODPECKER CAVITY TREES IN EASTERN TEXAS

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ABSTRACT.—We surveyed all known Red-cockaded Woodpecker (*Picoides borealis*) cavity trees (n = 514) in the Angelina National Forest in eastern Texas for Pileated Woodpecker (*Dryocopus pileatus*) damage. We compared the frequency of Pileated Woodpecker damage to Red-cockaded Woodpecker cavity trees in longleaf pine (*Pinus palustris*) habitat to damage in loblolly (*P. taeda*)-shortleaf (*P. echinata*) pine habitat. We also examined the effectiveness of restrictor plates in deterring Pileated Woodpecker enlargement of Red-cockaded Woodpecker cavities. Pileated Woodpecker damage was significantly greater in longleaf pine habitat than in the loblolly-shortleaf pine habitat in spite of census results showing similar abundance levels of Pileated Woodpeckers in the two forest types. We suggest that limited numbers of snags in the longleaf habitat may focus Pileated Woodpecker excavation on Red-cockaded Woodpecker cavity trees, whereas a greater amount of midstory vegetation in the loblolly-shortleaf pine habitat may serve to reduce visibility, thereby lowering Pileated Woodpecker detection and destruction of Red-cockaded Woodpecker cavities. Restrictor plates were very effective in preventing Pileated Woodpecker enlargement of cavities. While restrictor plates are useful for protecting Red-cockaded Woodpecker cavities, they should be used only in small populations when cavities are in short supply. The Pileated Woodpecker plays an important role, especially in the longleaf ecosystem which is a relatively cavity-barren environment, by providing nesting sites for larger secondary cavity users, such as American Kestrels (*Falco sparverius*), Eastern Screech-Owls (*Otus asio*), and fox squirrels (*Sciurus niger*). *Received 7 Jan. 1998, accepted 20 April 1998.*

The federally listed endangered Red-cockaded Woodpecker (*Picoides borealis*; USDI 1970) is endemic to the southeastern United States (Jackson 1971), and is unique because of its dependence on living pine trees in which it excavates roost and nest cavities (Steirly 1957). The pines used as cavity trees are generally mature, because the woodpeckers need heartwood (non-living xylem) large enough in diameter to house a cavity and sufficient time for fungus (*Phellinus pini*) to decay the heartwood for excavation (Jackson and Jackson 1986, Conner and O'Halloran 1987, DeLotelle and Epting 1988, Rudolph and Conner 1991). Young trees usually have thicker sapwood (living xylem that surrounds the heartwood and actively conducts resin) which means a proportionally smaller diameter heartwood (Conner et al. 1994).

The ability to excavate cavities in living pines was likely an evolutionary advantage in the frequently burned pine savannas where snags (standing dead trees that are used for nesting by most primary cavity nesters such as woodpeckers) are short-lived and hardwood midstory is infrequent or absent as a result of frequent fires. It can take several years for Red-cockaded Woodpeckers to fully excavate cavities in living pines but these cavities often last for decades (Conner and Rudolph 1995). Upon cavity completion, the Red-cockaded Woodpecker excavates shallow holes into the xylem, termed resin wells, which are worked regularly to stimulate copious resin flow (Ligon 1970, Dennis 1971). Resin flow may serve to protect cavities from predators and some cavity competitors (Dennis 1968, 1971; Ligon 1970; Jackson 1978; Rudolph et al. 1990). The Red-cockaded Woodpecker can be viewed as a keystone species in the southern pine ecosystem because of its ability to produce cavities in a relatively cavity-barren environment (Conner et al. 1997b). This has a positive impact on faunal diversity by providing cavities for secondary cavity users (Rudolph et al. 1990, Conner 1995, Conner et al. 1997a).

The old living pines and frequently burned ecosystem devoid of midstory that once gave the Red-cockaded Woodpecker an ecological

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advantage are now limiting factors because of their scarcity. Current management practices often involve short timber rotations which reduce the number of old trees available for cavity excavation (USDI 1985). Natural fire also has been suppressed allowing hardwood midstory encroachment that causes cluster abandonment (Conner and Rudolph 1989, Loeb et al. 1992). Short rotations and fire suppression are known to be associated with Red-cockaded Woodpecker population declines (Conner and Rudolph 1989, Costa and Escano 1989), and the effects of predators, competitors, and cavity-tree mortality are likely to be magnified in the small, isolated populations that exist today (Jackson 1974, 1978; Conner et al. 1991; Laves 1996).

In Texas, cavity-tree mortality and the effects of cavity damage caused by competitors are a serious concern for managers trying to aid in the recovery of the Red-cockaded Woodpecker. In this paper we examine the damage caused by Pileated Woodpeckers (*Dryocopus pileatus*) to Red-cockaded Woodpecker cavities and evaluate a technique used to prevent the damage. We also evaluate how Pileated Woodpecker damage to cavity trees is influenced by pine forest type, openness of forest, and the availability of snags.

STUDY AREA AND METHODS

Our study site was the Angelina National Forest (62,423 ha; 31° 15′ N, 94° 15′ W) in eastern Texas. The northern portion of the forest is dominated by loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines, while the southern portion, is predominately longleaf pine (*P. palustris*). The National Forest is divided in half by the Sam Rayburn Reservoir, isolating the northern and the southern Red-cockaded Woodpecker subpopulations from each other. The two halves of the forest are treated with prescribed burns at irregular intervals. The southern portion is burned at a higher frequency than the northern probably because the longleaf habitat is easier to burn. All cavity-tree clusters on both portions of the National Forest contain both natural and artificial cavities. Natural cavities are excavated completely by the Red-cockaded Woodpecker. Artificial cavities are provided by U.S. Forest Service personnel and come in two types: inserts (Allen 1991) and a modification (Taylor and Hooper 1991) of Copeyon's (1990) drilled cavity technique.

To evaluate the impact of Pileated Woodpeckers on natural Red-cockaded Woodpecker cavities we examined only living, Red-cockaded Woodpecker trees that were not equipped with restrictor plates [a steel plate nailed to the cavity tree to deter enlargement of Red-cockaded Woodpecker cavities (Carter et al. 1989)] 1984–1996. Trees that contained one or more unrestricted, natural cavities were used in the analysis. Cavities with entrances exceeding 70 mm in diameter are typically not used by Red-cockaded Woodpeckers and were assumed to have been enlarged by Pileated Woodpeckers (Rudolph et al. 1990). No other vertebrate in eastern Texas is likely to enlarge Red-cockaded Woodpecker cavities to this extent (pers. obs.).

All cavity trees (natural and artificial) were checked for evidence of Pileated Woodpecker excavation at Red-cockaded Woodpecker cavities and on other areas of the bole in December 1996. Pileated Woodpecker excavations were identified as coarsely-chiseled rectangular holes pecked through the bark into the xylem of cavity trees. Pileated Woodpecker excavations and cavity enlargement were combined and considered as evidence of Pileated Woodpecker occurrence for the analysis. We tested the null hypothesis that the frequency of Pileated Woodpecker excavation and cavity enlargement in cavity trees in loblolly-shortleaf pine habitat and longleaf pine habitat is equal using χ^2 analyses ($P = 0.05$) in a 2×2 contingency table. By calculating the percentage of trees damaged per year using "cavity tree years," as a measure of cavity tree availability, we eliminated bias resulting from differences in cavity tree availability between the two habitats.

Fifty-eight of the cavity trees we examined were fitted with 66 restrictor plates by U.S. Forest Service personnel. Some restrictor plates were placed over previously enlarged cavities ($n = 4$) in an attempt to repair them; such cavities were disregarded in the analysis examining the effectiveness of restrictor plates. Dead trees (6 trees) with restrictor plates (8 cavities) were not used in the analysis because they were potentially more attractive to Pileated Woodpeckers than live pines. We tested the null hypothesis that the rate of cavity enlargement in cavities with restrictor plates ($n = 54$) and unprotected natural cavities without restrictor plates ($n = 276$) is equal by use of a χ^2 analysis ($P = 0.05$) in a 2×2 contingency table.

To evaluate relative abundance of Pileated Woodpeckers within the loblolly-shortleaf pine habitat and longleaf pine habitats, we censused the birds using 5-min point counts during winter (1 January to 15 February) and spring (1 May to 15 June) in 1995 and 1996. Twenty sites in each habitat type were censused six times per season. Sampling was conducted one half hour before sunrise to 3 hours post sunrise. Sampling was not conducted during heavy rain or excessive winds (>20 km/h). We used a two-tailed t-test to compare Pileated Woodpecker abundance in the two habitat types.

To obtain a measure of midstory openness and availability of snags we randomly selected and sampled vegetation in 160, 11.2 m radius plots (0.04 ha) in each habitat type [as described by James and Shugart (1970) and Conner (1980, 1983)]. We recorded the number of large snags (>32 cm DBH) and the total number of snags in each plot. We also recorded the number of

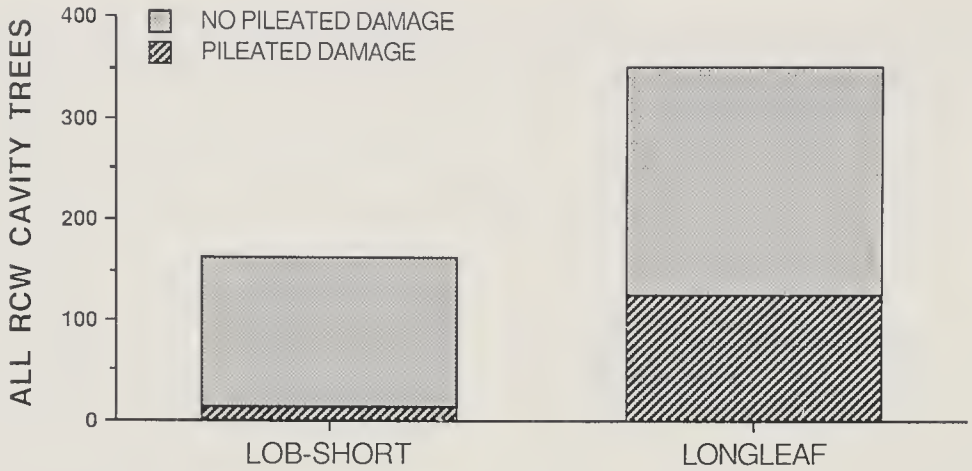

FIG. 1. The number of Red-cockaded Woodpecker cavity trees on the Angelina National Forest damaged by Pileated Woodpeckers (cavity enlargement or other excavations) in loblolly-shortleaf pine habitat compared to longleaf pine habitat ($\chi^2 = 41.2$, $P < 0.001$).

sapling (5–16 cm DBH) and pole (17–32 cm DBH) hardwoods and pines in each plot. Two-tailed *t*-tests were used to compare snag availability and midstory openness between the loblolly-shortleaf pine and the longleaf pine forest types. All analyses were calculated using PC-SAS (SAS Institute, Inc. 1988).

RESULTS

Pileated Woodpeckers regularly excavated into Red-cockaded Woodpecker cavity trees and enlarged cavity entrances; 27.2% (140 of 514 cavity trees, both habitat types combined) showed some evidence of Pileated Woodpecker damage. Pileated Woodpecker damage to Red-cockaded Woodpecker cavity trees was significantly greater in longleaf pine habitat than in loblolly-shortleaf pine habitat ($\chi^2 = 41.2$, $P < 0.001$; Fig 1). In the longleaf pine habitat type 35.8% (126 of 352) of the cavity trees showed signs of Pileated Woodpecker excavation whereas 8.6% (14 of 162) of the cavity trees showed signs of woodpecker excavations in the loblolly-shortleaf pine habitat. About 4.8% of all cavity trees in the longleaf pine habitat were damaged annually by Pileated Woodpeckers compared to 1.3% in the loblolly-shortleaf pine habitat.

Two hundred nineteen natural cavity trees contained 276 cavities without restrictor plates. Cavity enlargement occurred in 41.3% (114 of 276) of all unrestricted cavities. Pileated Woodpeckers enlarged Red-cockaded Woodpecker cavities at a significantly greater rate in longleaf pine habitat than loblolly-shortleaf pine habitat ($\chi^2 = 31.5$, $P < 0.001$; Fig 2). In longleaf pine habitat 50.7% (106 of 209) of the unrestricted cavities were enlarged whereas only 11.9% (8 of 67) were enlarged in loblolly-shortleaf pine habitat. Approximately 2.8% of the cavity trees in the longleaf pine habitat were enlarged by Pileated Wood-

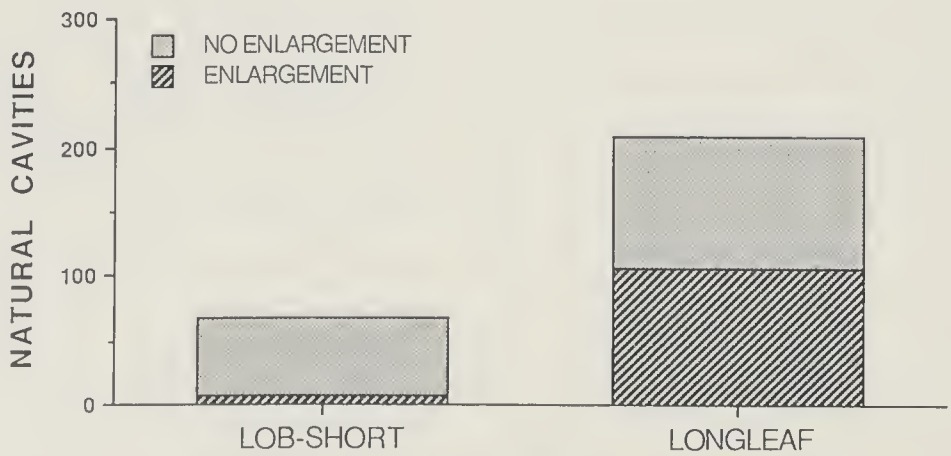

FIG. 2. The number of natural Red-cockaded Woodpecker cavities without restrictor plates on the Angelina National Forest enlarged by Pileated Woodpeckers in loblolly-shortleaf pine habitat compared to longleaf pine habitat ($\chi^2 = 31.47$, $P < 0.001$).

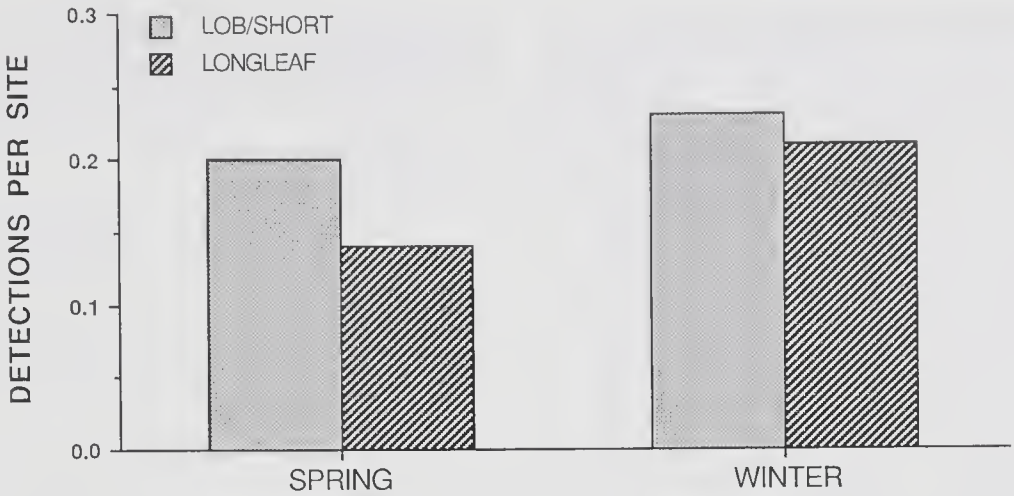

FIG. 3. The mean number of Pileated Woodpeckers detected at each site in loblolly-shortleaf pine habitat compared to longleaf pine habitat during spring (t = 1.31, $P > 0.05$) and winter (t = 0.36, $P > 0.05$) surveys.

peckers annually compared to only 0.8% enlargement in the loblolly-shortleaf pine habitat.

Restrictor plates (n = 54) were very effective in preventing enlargement by Pileated Woodpeckers as compared to unprotected cavities (χ^2 = 31.0, $P < 0.001$). In only one instance were Pileated Woodpeckers able to destroy a cavity fitted with a restrictor plate. The Pileated Woodpecker excavated a second entrance above the restrictor plate exposing the cavity above the original cavity entrance.

Abundance estimates from point counts revealed that Pileated Woodpeckers were similarly abundant in the two pine habitat types (Fig 3). We failed to detect differences between habitat types in Pileated Woodpecker abundance during both winter (t = 0.355, $P > 0.05$) and spring (t = 1.310, $P > 0.05$).

There were significantly more and larger snags in loblolly-shortleaf pine habitat than in longleaf pine habitat ($P < 0.001$; Table 1). The mid-story components (sapling and pole-size pine and hardwood trees) were also significantly more abundant in loblolly-shortleaf pine habitat than longleaf pine habitat ($P < 0.001$; Table 1).

DISCUSSION

Many Red-cockaded Woodpecker cavity trees in the Angelina National Forest were damaged by Pileated Woodpeckers. Because a large population of Pileated Woodpeckers is present across the forest, the difference in the amount of Pileated Woodpecker damage between the longleaf pine habitat and the loblolly-shortleaf pine habitat is surprising.

At least two factors may account for the differences in Pileated Woodpecker damage to Red-cockaded Woodpecker cavity trees between the two habitat types. We suggest that the relatively low number of snags in the longleaf habitat as a result of frequent burning and longer lived longleaf pine trees may focus

TABLE 1. Habitat comparisons between longleaf habitat and loblolly-shortleaf habitat.

Habitat[b] components	Lob-Short[a]		Longleaf[a]			
	$\bar{x}$	(SD)	$\bar{x}$	(SD)	t	P
TOTSNAG	1.95	1.97	0.25	0.55	10.539	<0.001
LRGSNAG	0.51	1.07	0.09	0.31	4.753	<0.001
SAPLHWD	9.07	5.60	0.53	0.91	19.045	<0.001
POLEHWD	1.48	1.33	0.09	0.20	13.114	<0.001
SAPLPIN	6.67	10.04	2.21	1.57	5.552	<0.001
POLEPIN	1.94	1.69	0.92	0.74	7.014	<0.001

[a] Data collected from 160 0.04 ha plots in each habitat.

[b] The habitat components sampled are as follows: (TOTSNAG = the total number of snags in the plot, LRGSNAG = the number of large snags in the plot, SAPLHWD = the number of sapling hardwoods in the plot, POLEHWD = the number of pole-sized hardwoods in the plot, SAPLPIN = the number of sapling pines in the plot, and POLEPIN = the number of pole-sized pines in the plot).

more of the attention of Pileated Woodpeckers on Red-cockaded Woodpecker cavity trees than in the loblolly-shortleaf pine habitat where snags are more abundant. Pileated Woodpeckers are known to use snags extensively for foraging and excavating roost and nest cavities (Conner et al. 1975, Kilham 1976, Bull and Meslow 1977, Conner 1980, Bull 1987). We also suggest that the openness of the frequently burned longleaf pine habitat may allow Red-cockaded Woodpecker trees to be more easily detected by Pileated Woodpeckers than trees in the infrequently burned loblolly-shortleaf pine habitat.

The reasons why Pileated Woodpeckers excavate holes in Red-cockaded Woodpecker cavity trees and enlarge cavities still are poorly understood. Pileated Woodpeckers only infrequently use such trees for roosts or nests (Conner et al. 1996). We suggest that Pileated Woodpeckers are attracted by excavations of other woodpeckers, in this case Red-cockaded Woodpecker cavities, and begin excavating possibly for either foraging or nesting. We also suggest that the sapwood is likely excavated in the process of enlarging the cavity chamber causing copious amounts of sticky resin to flow at the excavation site or into the cavity, and that this may discourage Pileated Woodpeckers from completely excavating a cavity. Although these enlarged cavities may not be fully excavated by the Pileated Woodpeckers, the amount of enlargement is usually sufficient for other cavity nesters.

Restrictor plates effectively prevented Pileated Woodpecker enlargement of Red-cockaded Woodpecker cavities. However, we caution against using restrictor plates on all Red-cockaded Woodpecker cavities. Although the Red-cockaded Woodpecker plays an important role in longleaf pine ecosystems by providing cavities for smaller secondary cavity nesters, the Pileated Woodpecker may play an equally important role by enlarging Red-cockaded Woodpecker cavities and providing nest sites for larger secondary cavity nesters, such as American Kestrels (*Falco sparverius*), Eastern Screech-Owls (*Otus asio*), and fox squirrels (*Sciurus niger*; Conner et al. 1997a). While we know that restrictor plates are a good management tool that may potentially be useful in recovering smaller Red-cockaded Woodpecker populations, we also suggest that Pileated Woodpeckers should be allowed to enlarge cavities for larger secondary cavity nesters in areas where Red-cockaded Woodpecker populations are stable, as a way to maintain natural faunal diversity.

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LIMITED GEOGRAPHIC VARIATION IN THE VOCALIZATIONS OF A NEOTROPICAL FURNARIID, *SYNALLAXIS ALBESCENS*

CATHERINE LINDELL[1,2]

ABSTRACT.—I recorded and analyzed vocalizations of *Synallaxis albescens* from three populations in Venezuela, two continental and one island, to assess the extent of geographic variation for a species of the family Furnariidae. Previous work on geographic variation in suboscines has focused on species of the Tyrannidae. I also tested the sound environment hypothesis. From nine vocalization characters I created discriminant functions that best separated the three populations. I then used classification analyses to determine how well the discriminant function models assigned individuals to their home populations. Classification analyses using discriminant functions created from first songs of recorded individuals correctly assigned individuals to their home populations 74.1% of the time and 66.7% of the time for functions created from arbitrarily chosen sixth songs. The island population was significantly more variable than either of the continental populations for the first syllable length but not for the frequency-modulated portion of the second syllable. The results demonstrate that geographic variation exists among populations although a sufficient amount of similarity prevents unequivocal classification of ¼ to ⅓ of individuals to their home populations. The results regarding vocalization variability provide weak support for the sound-environment hypothesis. *Received 30 June 1997, accepted 9 Feb. 1998.*

The avian order Passeriformes comprises two suborders, the oscines, suborder Passeri, and the suboscines, suborder Tyranni. The oscines developed the ability to learn vocalizations and now produce songs that are strongly influenced by environmental experience (Kroodsma and Baylis 1982). In contrast, the suboscines do not demonstrate vocal learning and generally produce songs that are stereotyped and little affected by the environment (Nottebohm 1972). For example, laboratory work with a suboscine species, the Eastern Phoebe (*Sayornis phoebe*) showed that its song was relatively unaffected by environmental influence (Kroodsma 1985, 1989; Kroodsma and Konishi 1991).

One result of the flexibility of the oscine vocal learning process is geographic variation of songs within species (Marler and Tamura 1962; reviewed in Mundinger 1982, Shy 1983, Tubaro et al. 1993, Tubaro and Segura 1995). If the lack of learning by the Eastern Phoebe extends to the majority of suboscines, the expectation is that their songs will not vary geographically to the extent observed in oscines because the environment will be unable to influence a learning process. This reasoning does not preclude the possibility that geographic variation may arise through restricted gene flow between populations, genetic drift, or natural selection for "fitting" vocalizations to the environment, but it does remove a potentially major source of variation. Studies that systematically investigated geographic variation in suboscine song have found little evidence that it exists, although the studies have all involved species of the family Tyrannidae (Lanyon 1978, Payne and Budde 1979, Johnson 1980). The present analysis is the first systematic investigation of geographic variation in the vocalizations of a Furnariid.

In this study I also compare the variability of vocalizations of an island population with that of two mainland populations, allowing a test of Marler's (1960) sound environment hypothesis. This hypothesis predicts that species inhabiting areas with few other species, the island population in this case, will be less constrained to produce rigid species-specific vocalizations than species inhabiting areas with many other competitors for vocal space, like the continental populations. The study species was the Pale-breasted Spinetail (*Synallaxis albescens*) which has an extensive distribution, ranging from Central America through central Argentina (Vaurie 1980).

STUDY AREA AND METHODS

Recordings of Pale-breasted Spinetails were made at three locations in Venezuela (Fig. 1). Hato Masaguaral, a wildlife preserve/cattle ranch in the state of Guarico

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FIG. 1. Sites where vocalizations were recorded.

in central Venezuela, is located at 8° 34′ N, 67° 35′ W. The second site was a rice farm, Puerto Miranda, in the state of Apure, 7° 54′ N, 67° 28′ W. The third site was the southern shore of the peninsula of Macanao on Margarita Island, off the northern coast of Venezuela, at 11° 00′ N, 64° 17′ W. Masaguaral is approximately 90 km from Miranda and 450 km from Margarita Island. Miranda is approximately 480 km from Margarita Island. Recordings were made at Masaguaral 19–20 April 1993, at Miranda 23 April 1993 and at Margarita Island, 29 April 1993. Eleven birds were recorded at Masaguaral, 10 at Miranda, and 6 at Margarita Island. Recordings were made passively, as I walked through sites and heard individuals singing. Male and female Pale-breasted Spinetails are monomorphic and it is likely that both sing as is the case with other Furnariids such as *Synallaxis brachyura* and *Phacellodomus rufifrons* (Skutch 1996). I used a TC-D5 Pro II Sony tape recorder and Dan Gibson P 650 parabolic microphone to make the recordings.

I made sonagrams for the first 11 songs per individual unless any of those songs did not produce a legible figure. When sonagrams were not legible, successive songs were used to obtain a total of 11 songs per bird. For one bird of the Margarita Island population only nine songs were usable. The sonagrams were produced with a Kay Elemetrics DSP Sonagraph, Model 5500. Time measurements were taken from sonagrams with a 300 Hz filter bandwidth and frequency measurements from sonagrams with a 59 Hz filter bandwidth. Following previous studies (Payne and Budde 1979, Johnson 1980, Kroodsma 1984, Baptista and Schuchmann 1990, Handford and Lougheed 1991, Tubaro and Segura 1995), I measured a number of variables for each song: the frequency immediately before the abrupt rise in frequency near the end of the first syllable (F1), the maximum frequency of the abrupt rise (F2), the maximum frequency of the second syllable (F3), the duration of the first syllable excluding the abrupt rise in frequency toward the end of the syllable (T1), the duration of the first syllable (T2), the duration of the interval between the first and second syllables (T3), the duration of the second syllable (T4), the duration of the first five frequency modulations after the maximum frequency of the second syllable (T5), and the duration of the entire vocalization (T6; Fig. 2).

Measurements taken from the first recorded songs of each individual were used in analyses to determine whether the three populations had distinctive song characteristics that could be used to classify individuals as belonging to one population or another. Similar analyses were carried out with the arbitrarily chosen sixth songs and the results using the first and sixth songs were compared. For the above models, I used

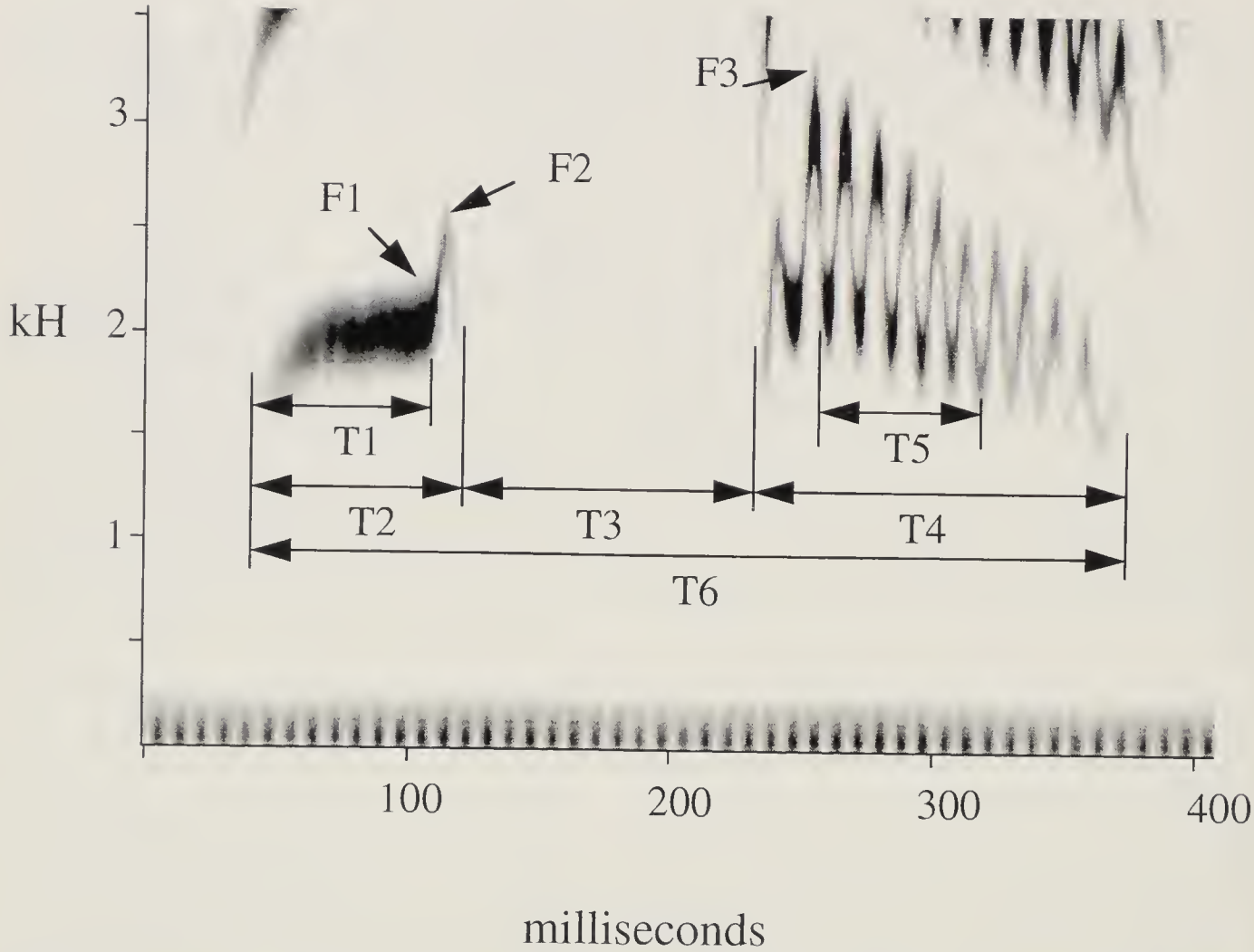

FIG. 2. Temporal and frequency variables that were measured from sonagrams of vocalizations of *Synallaxis albescens*.

stepwise Multivariate Analysis of Variance procedures to choose the song characteristics that could be used to create discriminant functions (Rencher 1995). The discriminant functions are linear combinations of the chosen variables that provide the best separation between groups. Once I determined the variables to be used in each model, the discriminant analyses were conducted. The same models were then used in classification analyses to determine how well the models classified an individual as belonging to a particular population.

Coefficients of variation provide a means to compare the variability of a character across populations. To test the sound environment hypothesis I determined coefficients of variation for the two uncorrelated vocal characters that were most useful in discriminating among the populations. Since the island population of Pale-breasted Spinetails shares vocal space with only one half the number of species as the mainland populations, the expectation was that the vocal characters should be more variable for the island population. All statistical analyses were performed with SYSTAT 5.2 for the Macintosh (SYSTAT 1992).

RESULTS

The song of *Synallaxis albescens* is composed of two notes and is usually repeated frequently by an individual. The song shows similarities to those of the Eastern Phoebe and the Willow Flycatcher (*Empidonax traillii*). Two to three harmonics were visible in most spectrograms with more energy typically concentrated in the second harmonic than in the fundamental frequency. Measurements of the nine variables for individuals of the three populations are given in Table 1.

The duration of the first syllable, the duration of the first syllable excluding the abrupt rise in frequency toward the end, the duration of the frequency-modulated portion of the second syllable, and the frequency near the end of the first syllable showed significant differences among populations in one-way ANOVAs using the first songs and then the sixth songs of individuals. However, some of these variables were significantly correlated. For first and sixth songs, the durations of the first syllable and the frequency-modulated portion of the second syllable were two uncorrelated

TABLE 1. Descriptive statistics for vocalizations of *Synallaxis albescens* from three populations.

Variable	Hato Masaguaral	Margarita Island	Puerto Miranda
No. individuals	11	6	10
T1[a]	88.25 ± 9.00[b]	93.45 ± 14.66	102.29 ± 12.88
T2	102.35 ± 9.00	107.42 ± 13.67	116.13 ± 12.70
T3	95.04 ± 8.23	103.79 ± 14.71	92.16 ± 7.45
T4	166.41 ± 17.65	167.61 ± 9.66	172.27 ± 16.64
T5	53.85 ± 5.48	58.90 ± 2.78	51.75 ± 3.45
T6	360.99 ± 12.75	377.80 ± 32.72	380.64 ± 30.61
F1[c]	2320.00 ± 151.46	2145.25 ± 171.50	2294.18 ± 143.07
F2	2949.75 ± 175.96	2672.83 ± 301.08	3027.09 ± 400.02
F3	3249.18 ± 212.82	3204.92 ± 229.47	3320.55 ± 249.25

[a] T1 is the duration of the first syllable, excluding the abrupt rise in frequency at the end of the syllable; T2 is the duration of the first syllable; T3 is the duration of the interval between the first and second syllables; T4 is the duration of the second syllable; T5 is the duration of the first five frequency modulations after the maximum frequency of the second syllable; T6 is the duration of the entire vocalization; F1 is the frequency immediately before the abrupt rise in frequency near the end of the first syllable; F2 is the maximum frequency of the abrupt rise; F3 is the maximum frequency of the second syllable. Time variables are in milliseconds.

[b] Values are mean ± standard deviation. Means are based on 11 songs per individual except for one individual from the Margarita Island population for which I used 9 songs. I calculated a mean for each individual and then calculated a second order mean for each population using the individual means.

[c] Frequency variables are in Hertz.

variables that showed significant differences among populations ($F_{2,24}$ = 4.66, $P < 0.025$, and $F_{2,24}$ = 4.50, $P < 0.025$, respectively, for first songs; $F_{2,24}$ = 3.54, $P < 0.05$, and $F_{2,24}$ = 4.05, $P < 0.05$, respectively, for sixth songs). For first and sixth songs, the duration of the first syllable did not differ between the populations of Masaguaral and Margarita Island or between the populations of Miranda and Margarita Island, although it was significantly longer for the Miranda population compared to the Masaguaral population (Tukey-Kramer test for unplanned comparisons among means: $P > 0.05$, > 0.05, and = 0.02, respectively, for first songs; $P > 0.05$, > 0.05, and = 0.04, respectively, for sixth songs). The duration of the frequency-modulated portion of the second syllable did not differ between the populations of Masaguaral and Margarita Island or between the populations of Masaguaral and Miranda, although it was significantly longer for the population of Margarita Island compared to the population of Miranda (Tukey-Kramer test for unplanned comparisons among means: $P > 0.05$, > 0.05, and = 0.02, respectively, for first songs; $P > 0.05$, > 0.05, and = 0.03, respectively, for sixth songs).

TABLE 2. Discriminant models constructed to distinguish vocalizations from three populations.

Variables	Correlation with discriminant function 1	Correlation with discriminant function 2
First Songs		
T2[a]	0.61355	0.78965
F1	0.48997	−0.87174
Sixth Songs		
T5[b]	−0.48905	0.89350
T2	0.31557	0.40472
F1	0.39433	−0.76115

[a] T2 is the duration of the first syllable; F1 is the frequency immediately before the abrupt rise in frequency near the end of the first syllable. Both variables make significant contributions to model, T2 at $P < 0.025$ and F1 at $P < 0.025$. Model has overall Wilks' Λ of 0.492, $F_{4,46}$ = 4.90, and $P < 0.005$.

[b] T5 is the duration of the first five frequency modulations after the maximum frequency of the second syllable. All three variables make significant contributions to model, T5 at $P < 0.05$, T2 at $P < 0.01$, and F1 at $P < 0.05$. Model has overall Wilks' Λ of 0.364, $F_{6,44}$ = 4.82, and $P < 0.001$.

Stepwise MANOVA variable selection and discriminant analyses for the first songs revealed that the duration of the first syllable and the frequency near the end of the first syllable were most important in distinguishing individuals from different populations. For the sixth songs, the duration of the frequency-modulated portion of the second syllable, the duration of the first syllable, and the frequency near the end of the first syllable were most important (Table 2). Subsequent classification analyses using the discriminant models correctly classified an individual bird to its home population 74.1% of the time for the first song model and 66.7% of the time for the sixth song model.

For the duration of the first syllable, the Margarita Island population had a significantly greater coefficient of variation than either

the Masaguaral population ($\bar{x}$ = 4.74 ± 0.62% SD vs. 3.67 ± 1.40%, respectively; Mann-Whitney *U*-test; N_1 = 11, N_2 = 6, U = 55, P < 0.025) or the Miranda population (2.87 ± 1.13%, Mann-Whitney *U*-test; N_1 = 10, N_2 = 6, U = 55, P < 0.005). For the coefficients of variation of the duration of the frequency-modulated portion of the second syllable, there were no significant differences between the Margarita Island and Masaguaral populations (2.28 ± 2.07% vs 1.76 ± 0.81%, respectively; Mann-Whitney *U*-test; N_1 = 11, N_2 = 6, U = 34, P > 0.05) or between the Margarita Island and Miranda populations (1.74 ± 0.61%; Mann-Whitney *U*-test: N_1 = 10, N_2 = 6, U = 34, P > 0.05).

DISCUSSION

Previous researchers of furnariid vocalizations have concluded that little, if any, geographic variation exists, although the conclusions were not based on systematic analyses of songs (Vaurie and Schwartz 1972, Vaurie 1980). For example, Vaurie and Schwartz (1972) presented sonagrams for various members of the genus *Synallaxis* but their conclusion of no variation in the song of several species, including *S. albescens,* was based on "the extensive field experience of Schwartz". With regard to suboscines of families other than the Furnariidae, Payne and Budde (1979), in their investigation of song differences and distance between territorial Acadian Flycatchers (*Empidonax virescens*), reported a lack of correlations between the degree of similarity of any of the song characters and distance between birds, although they conducted their study over a limited geographic scale (< 30 km). Lanyon (1978) in a revision of the genus *Myiarchus,* reported no geographic variation in vocalizations for 7 of the 11 species studied. For 1 of the 11 species he had no data, and of the 3 for which he did report some variation, 2 showed variation in carrier frequency that he found to be inversely correlated with body size (bigger body = lower frequency). The geographic variation Johnson (1980) described for two other species of flycatchers, *E. difficilis* and *E. flavescens,* may be a result of interspecific, rather than intraspecific variation (Kroodsma 1988). The results here demonstrate some identifiable differences between the populations although not all the patterns are consistent with the expectation that the closest populations, Masaguaral and Miranda, should be the most similar. Although these populations were similar in the duration of the frequency-modulated portion of the second syllable, they were significantly different in the duration of the first syllable. The Margarita Island population showed no differences from the Masaguaral population in these two variables while it did differ from the Miranda population in the duration of the frequency-modulated portion of the second syllable. These results indicate that some vocal characters differ among populations, but that the patterns of difference are not consistent from character to character, and that distance between sites is not a good predictor of the degree of similarity between populations. It is unlikely that population differences can be attributed to different motivational states because all individuals were recorded during approximately the same time of year, late in the dry season before breeding had begun.

The discriminant models demonstrate that combinations of variables can be used to classify individuals to one population or another, although not with a great deal of accuracy; 74.1% of individuals were correctly classified with the first song model and 66.7% were correctly classified with the sixth song model. An observer is hard put to distinguish differences among the populations in the field (pers. obs.), although a few subtle differences among populations were evident from the sonagrams. In contrast, research of oscine vocalizations sometimes reveals striking patterns of song differences over distance (Marler and Tamura 1962, McGregor 1980, Rothstein and Fleischer 1987). Baptista and King (1980) for example, found seven song types and numerous distinctive variations of these types for White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the western U.S. The results presented here indicate that the variability that exists between populations is less than that found in several oscine species that have been studied, and support the idea that environmental influence on song is limited.

The greater variability of the duration of the first syllable for the Margarita Island population, compared to either of the mainland populations, supports the sound environment hypothesis of Marler (1960) that predicts vocal-

izations are less species-specific in environments with fewer other species. Approximately 147 resident species occur on Margarita Island (Yepez Tamayo 1963), while nearly 300 occur in central Venezuela, where the Masaguaral and Miranda populations are located (Thomas 1979). Kroodsma and coworkers (1987) found little support for the sound environment hypothesis in a comparison of the variability of songs of the Cocos Flycatcher (*Nesotriccus ridgwayi*) with songs of the closely related Mouse-colored Tyrannulet (*Phaeomyias murina*), which lives in a more species-rich environment. However, a comparison of the vocalizations of one species in several environments provides a stronger test of the hypothesis. The duration of the frequency-modulated portion of the second syllable, in contrast to the duration of the first syllable, was not more variable in the island population than the continental populations, indicating that different song characters vary in their flexibility. If the duration of the frequency-modulated portion of the second syllable is a more significant variable with regard to species-specific recognition than the duration of the first syllable, it may be that such characters are highly conserved, even in species-poor environments. A more definitive test of the hypothesis will include assessments of the importance of the characters to the birds' species-recognition abilities and determination of the strength and mechanisms of interspecific influences on song.

Suboscine families such as the Furnariidae and the Tyrannidae are speciose (>200 species and >350 species, respectively), yet several authors have suggested a link between vocal learning and high rates of speciation. Marler (1970) suggested that vocal learning was an evolutionary response to the demands of species-specific recognition in passerines, necessitated by high rates of speciation and high degrees of sympatry in the group. Kroodsma (1988) indicated that high speciation rates among oscines may be a result of vocal learning, if vocal learning promotes genetic isolation of populations. Nottebohm (1972:130) also recognized a relationship between rapid speciation and the ability to learn vocalizations, although he stated, "In no case is it possible to say whether vocal learning preceded and aided rapid speciation or resulted from it; the correlation between the two may be accidental." He also noted exceptions to the pattern of speciose groups being vocal learners, for example, the tyrannids and furnariids mentioned above. Ames (1971), in his analysis of syrinx characters and their relevance to passerine systematics, documented the uniform morphology of the oscine syrinx and the highly variable nature of the suboscine syrinx. While vocal learning, associated cultural evolution, and geographic variation in song may be linked to rapid speciation in oscines, perhaps morphological evolution of the syrinx and accompanying divergence in song is linked to high speciation rates in suboscine groups. The constraints of the evolutionary histories of the two groups may have resulted in different strategies to insure species-specific song and reproductive isolation.

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NEST-SITE SELECTION AND NESTING SUCCESS OF WOOD THRUSHES

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ABSTRACT.—We characterized nest sites and compared specific nest-site characteristics to nesting success for Wood Thrushes (*Hylocichla mustelina*) nesting in southeastern Pennsylvania in 1991. We determined if nests were placed in areas that differed from randomly selected points within a given tract of forest and compared specific nest-site characteristics for successful nests (those that produced at least one fledgling) and nests that failed because of predation. Wood Thrushes selected nest sites non-randomly within a tract of forest, and female Wood Thrushes built nests in areas that had a higher density of trees, higher canopy, higher density of shrubs, and higher average shrub height than randomly selected points. Specific nest-site characteristics had little effect on the ultimate success or failure of nests. The only specific nest-site characteristic included in a stepwise logistic regression model comparing successful and failed nesting attempts was the concealment of the nest from above and below. The average concealment of successful nests was greater than unsuccessful nests, but the model that included nest concealment did not give good fit to the data. Rather, a landscape-level feature, size of forest tract, had the greatest influence on the success and failure of nests for Wood Thrushes in this region. *Received 10 Feb. 1997, accepted 20 April 1998.*

The Wood Thrush (*Hylocichla mustelina*) is a neotropical migrant that has undergone significant population declines in recent decades (Sauer et al. 1996). Poor reproductive success, particularly as a result of high rates of nest predation, has been cited as one probable cause of the decline (Robinson 1992, Roth and Johnson 1993, Hoover et al. 1995). Identification of specific habitat features associated with nest sites and nesting success, and a calculation of the probability of success given certain characteristics are needed in order to develop long-term strategies for reversing declines in populations of Wood Thrushes and other neotropical migrants (Martin 1992). Also, information on nest-site selection may be applied to management of habitat for this and other species of neotropical migrants.

General characteristics of the forest habitat where Wood Thrushes are found during the breeding season have been described by other researchers (Bertin 1977, James et al. 1984, Roth 1987). In addition, other researchers have documented the influence of landscape features such as forest patch size and proximity to edge habitat on the probability of nest success (e.g., Robinson 1988, 1992; Hoover et al. 1995). In this study, we looked at nest-site selection by Wood Thrushes in two different ways. We first determined whether or not Wood Thrushes, within the forest, used particular areas for nesting based on the structure of the vegetation. We then measured microhabitat characteristics of successful nests and nests that were lost to predators. Our specific objectives were to: (1) determine the characteristics of the vegetation that influenced the probability that a site would be used for nesting by a Wood Thrush, and (2) determine whether or not microhabitat characteristics at the nest site influenced the probability of nesting success.

METHODS

During the summer of 1991, data for this study were collected as part of a larger study of the nesting success of Wood Thrushes in a fragmented forest landscape in Berks County, Pennsylvania (see Hoover et al. 1995 for a general description of the study sites). Characteristics of the vegetation were measured on nine tracts of forest (study sites) ranging from 16.4 ha to more than 500 ha (Table 1). Nine randomly-selected points were established on each tract of forest by placing a 150 × 150 m scale grid over a map of each tract, assigning a number to each grid point, and using a random numbers table to select the points. Points were separated by a minimum of 150 m and, when possible, were located at least 60 m from the nearest forest edge.

We collected vegetation data from each study site during July. We measured characteristics of the vegetation within a 0.04 ha circle centered on each of the nine points by using a modification of the James and Shugart (1970) method. We recorded the number of

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TABLE 1. Characteristics of the study sites in Berks County, Pennsylvania.

Study site	Forest area (ha)	Forest core area (ha)[a]	Distance to contiguous forest (km)[b]	Percentage forested area within a 2 km radius[c]
Owl's Head	>10,000[d]	>10,000	0.0	96.5
River of Rocks	>10,000[d]	>10,000	0.0	97.2
Spitzenberg	126.5	45.3	2.4	35.7
Gun Club	103.4	47.8	10.6	50.5
Snook	79.8	6.5	11.2	42.7
Kunkle	23.4	2.5	9.1	20.9
Kehl	19.4	0.04	3.3	27.4
Lilienthal	18.7	1.4	11.8	42.7
Dixon	16.4	2.3	7.0	22.9
Bauscher[e]	9.2	0.5	6.7	23.4

[a] Area of forest that was >100 m from an edge (Temple 1986).
[b] Nearest forest >10,000 ha.
[c] Measured from the center of each study site.
[d] Nest searching occurred primarily within a 40 ha plot.
[e] Study site used only for analysis of nesting success related to nest-site characteristics.

trees (total number of trees greater than 5.1 cm dbh per 0.04 ha circle), basal area (total basal area per 0.04 ha circle), and canopy height (estimated average height of the trees within each 0.04 ha circle). We tallied the number of shrub stems along two arm-length perpendicular transects (approximately 2 m wide) that bisected the 0.04 ha circle, and recorded the mean height of the shrubs. We measured percent cover with an ocular tube in two height classes (ground cover between 0.0 and 0.5 m and canopy cover greater than 10 m) at 20 randomly-selected points within each 0.04 ha circle and calculated the mean percent cover for each height class.

Study grids (30 m × 30 m) were established on each study site. Territories of Wood Thrushes were spot-mapped in relation to the grid points and we found nearly all nests within these territories. We searched for Wood Thrush nests on 10 study sites between 1 May and 1 August, 1991. We included data collected from the additional study site (Bauscher) in the analysis of specific nest-site characteristics and nesting success but not in the nest-site selection analysis. We searched over the entire tract of forest on the smaller study sites (those less than 100 ha) and on a 40 ha portion of the larger study sites. After a nest was found, we recorded its status every four days until the nesting attempt either failed or young fledged from the nest. Nests were visited more frequently near the expected time of fledging to verify fledging. We used a pole with an attached mirror (Parker 1972) to monitor the contents of nests located up to 8 m from the ground. A nesting attempt was classified as successful if at least one Wood Thrush fledged (Harris et al. 1963).

The number of Wood Thrush nests found per study site ranged from 6–33. We randomly selected five Wood Thrush nests on each study site and measured the characteristics of the vegetation within a 0.04 ha circle centered at each nest, using the modified James and Shugart (1970) method. If, on a given study site, we selected a nest that was located within 25 m of one of the nine randomly selected points, it was not used and another nest was selected in its place. We measured characteristics of the vegetation around the five nests on each study site in late July after all of the nests were no longer being used.

We also recorded seven nest-site characteristics for all Wood Thrush nests found. For each nest, specific nest-site characteristics were measured within two days of when the nest became inactive. We measured nest height, distance to forest edge [distance of the nest to the nearest external forest edge (with the exception of six nests on the Owl's Head site where the distances were measured to forest openings 0.4–0.8 ha)], dbh of supporting vegetation (diameter at breast height of the vegetation supporting the nest, averaged for vegetation with multiple stems), lateral distance of the nest from the main stem of the vegetation supporting the nest (measured from the center of the nest), and nest concealment indices (percentage of nest that was visible in a horizontal plane, a vertical plane, and combined horizontal and vertical planes).

We determined how well each nest was concealed by calculating an index of nest exposure both horizontally and vertically by using a modification of a white cover board (30 × 20 cm; Nudds 1977). On the cover board, we painted 10 yellow circles in two rows of 5. The circles were 5 cm in diameter, with centers spaced 6 cm apart. We placed the cover board directly on the north, south, east, west facing, top, and bottom sides of each nest. We recorded the number of circles completely visible from each direction at a lateral distance of 3 m from the cover board at the height of the nest, from 1 m above, and from ground level beneath the nest. Measurements were taken from ground-level beneath each nest to simulate concealment of nests from nest predators on the ground. Lateral and above-nest measurement distances were chosen to obtain a relative quantitative index of nest concealment

within close proximity to the nest. We defined the total number of circles completely visible from the four lateral directions as the horizontal exposure, and from above and below as the vertical exposure of the nest. We determined total exposure by summing values for horizontal and vertical exposure. We report all exposure measurements as percentage of circles visible (nest concealment is equal to percent exposure subtracted from 100).

In order to simultaneously evaluate the influence of multiple characteristics on the probability of a site being selected for nesting or on the probability of a nest being successful, we used stepwise logistic regression (SAS on a DOS computer: PROC LOGISTIC; SAS Institute Inc. 1990, 1995) with the nest-site variables (general vegetation or specific nest-site characteristics) included as independent variables and the possible responses (nest/no nest or success/failure) as the dependent variables. For the analysis of nest-site selection we used study site as a control variable to reduce the influence that differences in vegetation among study sites might have on the results. Similarly, we included size of forest tract as a control variable for the analysis of nesting success because we were aware of a significant positive correlation between forest area and nesting success (Hoover et al. 1995). In this way, we could determine whether or not any of the specific nest-site characteristics had a significant association with nesting success when controlling for forest area.

The best subset selection method (Hosmer and Lemeshow 1989) was used to find the best four models for all possible model sizes. These were then compared on the basis of the Hosmer-Lemeshow C (H-L) statistics, the Wald statistics for individual variables, the amount of change in the β coefficients between models (>20% considered important), and the size of the standard errors of the coefficients. Likelihood ratios were also compared between models with the same number of terms, and a χ^2 statistic using the likelihood ratios was used to compare models with different numbers of hierarchically arranged terms to select the best model for each analysis.

TABLE 2. Species of vegetation supporting 127 Wood Thrush nests found in Berks County, Pennsylvania, 1991.

Species	*n*	Percent of total
Spicebush (*Lindera benzoin*)	57	44.9
Witch hazel (*Hammamelis virginiana*)	21	16.5
Tartarian honeysuckle (*Lonicera tatarica*)	10	7.9
Black cherry (*Prunus serotina*)	8	6.3
Black tupelo (*Nyssa sylvatica*)	8	6.3
American beech (*Fagus grandifolia*)	3	2.4
Eastern hemlock (*Tsuga canadensis*)	3	2.4
Mapleleaf viburnum (*Viburnum acerifolium*)	3	2.4
Red maple (*Acer rubrum*)	3	2.4
Mountain laurel (*Kalmia latifolia*)	2	1.6
Rosebay rhododendron (*Rhododendron maximum*)	2	1.6
Sassafras (*Sassafras albidum*)	2	1.6
Sugar maple (*Acer saccharum*)	2	1.6
Multiflora rose (*Rosa multiflora*)	1	0.8
White ash (*Fraxinus americana*)	1	0.8
White mulberry (*Morus alba*)	1	0.8

RESULTS

We found 127 Wood Thrush nests on 10 study sites in 1991. Most of the nests (>85%) were found during the nest building, egg laying, or early incubation (days one through three) stage of the nesting cycle. One nest lost during a storm was not used for the analysis of nest-site characteristics and nesting success. Of the 126 nests, 76 were successful (at least one Wood Thrush fledgling produced) and 50 failed because of predation. We attributed all nesting failures to predation, with the exception of the nest destroyed during a storm. Thirty-six nests were preyed upon during incubation, and 14 during the nestling phase. Based on the condition of the nests and their contents following predation events, approximately 80% of nest predation events were attributed to either avian, snake, or small mammalian nest predators, and the remaining 20% to large arboreal mammals.

Nests were built in 16 species of vegetation including 8 species of shrub and 8 species of tree (Table 2). Nearly 77% of all nests were built in shrubs with 70% built in spicebush (*Lindera benzoin*), witch hazel (*Hammamelis virginiana*), or tartarian honeysuckle (*Lonicera tatarica*; Table 2). Black cherry (*Prunus serotina*) and black tupelo (*Nyssa sylvatica*) were the species of tree most often used for nest sites. Several of the trees that were used for nesting were either saplings or small trees (less than 10 cm dbh). Mountain laurel (*Kal-*

TABLE 3. Mean values for seven nest-site selection and seven specific nest-site location variables for Wood Thrushes nesting on study sites in Berks County, Pennsylvania, 1991.

Variable[a]	Mean	SD	Range
Characteristics of nest-site selection (n = 45 nests)			
Number of trees per 0.4 ha	42.6	18.1	7–95
Basal area (m^2)	2.7	0.8	0.31–3.74
Canopy cover[b] (%)	93.5	10.1	25–100
Canopy height (m)	24.1	4.7	10–33
Number of shrub stems	79.5	53.7	3–234
Shrub height (m)	2.5	0.4	0.6–4.6
Ground cover[b] (%)	80.0	26.5	5–100
Characteristics of specific nest-site location (n = 126 nests)			
Nest height (m)	2.2	1.1	1.0–6.5
Distance to edge (m)	61.3	50.3	1–300
Dbh of supporting vegetation (cm)	4.8	6.8	0.8–55.9
Distance from nest to main stem (cm)	7.6	23.6	0.0–182.9
Horizontal exposure[c] (%)	13.8	13.8	0–65
Vertical exposure[c] (%)	17.5	14.6	0–70
Total exposure[c] (%)	15.0	12.0	0–60

[a] See text for descriptions of variables.
[b] Statistical analyses were conducted using number of sightings, but results are reported as percentage of sightings.
[c] Statistical analyses were conducted using number of cover board circles completely visible, but results are reported as the percentage of circles visible.

mia latifolia), rosebay rhododendron (*Rhododendron maximum*), and eastern hemlock (*Tsuga canadensis*) were the only evergreens used by Wood Thrushes for nest sites. The means, standard deviations, and ranges of values for the nest site characteristics used for the nest site analysis and for the nesting success analysis are given in Table 3.

A four variable regression model best explained which sites were used for nesting when controlling for study site (Table 4). Wood Thrushes built nests in areas within the forest that had higher densities of trees, higher canopy heights, higher densities of shrub stems, and higher average shrub heights than randomly-selected points (Table 4). There were no interaction terms that met the criterion for inclusion. The model gave good fit to the data (H-L statistic = 4.3, df = 8, P = 0.83). When testing for the fit of a model, a high P-value indicates that the expected values from the model are not different from the observed values, hence the model is a good fit. The odds ratios (Table 4) evaluate the strength or magnitude of the association of the variables to the outcome (nest or no nest). The conditional odds ratios (Table 4) represent the change in likelihood of a nest being present

TABLE 4. Results of stepwise logistic regression analysis of vegetational characteristics in the vicinity of 45 randomly chosen Wood Thrush nests and 81 randomly chosen non-nest points on study sites in Berks County, Pennsylvania, 1991.

Variable[a]	β	P[b]	Odds ratio	Conditional odds ratio	Units[c]
Intercept	−14.814	—	—	—	—
Site	−0.0643	—	—	—	—
Number of trees	0.0766	0.0001	1.080	1.467	5.0
Canopy height	0.3578	0.0001	1.430	2.045	2.0
Number of shrub stems	0.0168	0.0123	0.017	1.188	10.0
Average shrub height	1.1562	0.0007	3.178	1.783	0.5

[a] See text for description of variables.
[b] P-value for significance of Wald χ^2.
[c] Units for conditional odds ratio (e.g., within the range of values for average shrub height, with an increase of 0.5 m, the probability of a nest being present increases by 1.8 times).

TABLE 5. Results of stepwise logistic regression analysis comparing specific nest-site characteristics between 76 successful and 50 failed Wood Thrush nests on study sites in Berks County, Pennsylvania, 1991.

Variable[a]	β	P[b]	Odds ratio	Units[c]
Intercept	0.3206	—	—	—
Forest area	0.0075	—	—	—
Vertical exposure[d]	−0.1852	0.011	0.831	5.0

[a] See text for description of variables.
[b] P-value for significance of Wald χ^2.
[c] Units for odds ratio (e.g., within the range of values for vertical exposure, with a 5% increase in exposure, the probability of nesting success decreased by 0.8 times).
[d] Statistical analyses were conducted using number of cover board circles completely visible, but odds ratio units are reported as a percentage (one circle = 5%).

for every unit change of a variable within the range of values for that variable (Table 3). For example, within the range of average shrub heights (0.6–4.6 m), the probability of a nest being present in a particular area within the forest increases by 1.8 times with every 0.5 m increase in average shrub height (given that Wood Thrushes are present on the site).

All Wood Thrush nests were within 6.5 m of the ground and were built as close to a forest edge as 1 m and as far away as 300 m. Most forest edges were with adjacent agricultural fields (>90%), some with highways or residential areas, and a few with natural openings (0.4–0.8 ha) within the forest. Nests were usually built near the main stem of the shrub or tree supporting the nest, and the main stem of the shrub or tree usually had a relatively small dbh (Table 3). For all nests, mean concealment was 86% laterally and 82% from above and below (but note the large ranges of values in Table 3). When controlling for forest tract size, the only variable significant enough to enter the model was vertical exposure (amount the nest is exposed from above and below; Table 5). The average nest concealment (percent exposure subtracted from 100%) above and below nests was approximately 85% and 75% for successful and failed nests, respectively. The model, however, lacked good fit to the data (H-L statistic = 16.5, df = 8, P = 0.036) and explained the variability in the nesting success poorly.

DISCUSSION

A variety of factors can potentially influence nest-site selection including availability of song perches, floristic composition, moisture regimes, amounts and kinds of feeding substrata, amounts of food, structure of the plant community, and risks of nest predation (Bertin 1977, Holmes et al. 1979, James et al. 1984, Steele 1993, Martin 1993a). When considering factors related to characteristics of vegetation within the forest, Wood Thrushes selected areas that had taller trees and taller shrubs than randomly selected sites. Bertin (1977) suggested that Wood Thrushes prefer to establish breeding territories in areas within the forest where there are taller trees because taller trees provide better (higher) song perches for males and an increased amount of leaf litter as a substrate for foraging. If this is true, then nest-site selection by females would also show the same tendency because they are building nests within the territories of the males. Tall shrubs were frequently used as nest sites possibly because they provided larger branches and a more stable structure for nests than shorter shrubs, although we did not test for this.

Nest sites were selected in areas within the forest where the density of trees was greater than random sites and possibly in response to the amount of leaf litter created by the larger number of trees. In addition, areas within the forest with larger numbers of tree and shrub stems could be indicative of a favorable moisture regime that influences the use of an area by Wood Thrushes (Bertin 1977).

Other researchers have suggested that shrub-nesting birds should preferentially select nest sites with higher shrub densities to reduce the risk of predation (Joern and Jackson 1983, Martin 1993b). Wood Thrushes nested in areas that had a higher density of shrubs than expected based on availability. Shrub density did not differ among the seven smaller sites but was significantly greater than on the two largest study sites (Hoover 1992). Nesting success was highest on the two largest sites where shrubs were lowest in density, (Hoover et al. 1995). This result suggests that increased shrub density itself did not increase nesting success in these forests. Shrub cover was scattered throughout all of our sites, and the relationship between density of shrubs and risk of predation may be more important in more open habitats where shrubs form discrete patches.

Of the several specific nest-site characteristics that might influence nesting success (e.g., concealment, nest height, proximity to habitat edge; Martin 1993b, Filliater et al. 1994), only the vertical exposure of the nest (visibility of the nest from above and below) was deemed significant in our analysis. In 29 of 36 studies summarized by Martin (1992), predation rates were lower at nests with greater concealment. Nest concealment may be particularly important in areas where corvids are suspected of being the major nest predators because corvids use visual cues to locate nests (Morrow and Silvy 1982, Westmoreland and Best 1985, Angelstam 1986, Yahner and Scott 1988, Patnode and White 1992). Although we were usually unable to identify the specific nest predators responsible for nest predation events, Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*) were present on all of our study sites and were most abundant on small sites where predation rates were highest (Hoover et al. 1995).

Angelstam (1986) found that visibility through the vegetation in the area around each nest was more important to nesting success than the visibility directly at the nest site. Bowman and Harris (1980) also found that increased levels of spatial heterogeneity around artificial ground nests increased predator search time and reduced the number of nests found by the nest predator. They concluded that spatial heterogeneity is more important than nest concealment. We did not measure spatial heterogeneity around the nest, but our method of measuring nest concealment did measure the visibility of the nest through the vegetation from a distance of 3 m laterally from four different directions. Also, by using a cover board, we eliminated the arbitrary estimation of nest concealment and obtained a quantitative value for nest concealment. We did not detect a difference in lateral concealment between successful and failed nests. It is possible that our measure of nest concealment was not at a spatial scale relevant to the particular nest predators in this region.

The lack of correlation between nest height and nest success may be due to the diverse predator community present in the study sites. The nest predator community consisted of a variety of birds, snakes, and small and large arboreal mammals (Hoover et al. 1995). Because of the diversity of potential nest predators, the techniques used by the nest predators when searching for prey are also diverse and, as a group, they would not be expected to detect nests at any one height better than another (Filliater et al. 1994). If there were only a few species of potential nest predators, or one species that specialized on a particular layer of the vegetation while foraging, then specific nest placement would be favored to avoid the limited search area of those particular nest predators.

Selection of a nest site near the forest edge may increase the risk of nest failure because of elevated rates of nest predation associated with "edge effects" (e.g., Gates and Gysel 1978). However, other researchers have failed to detect differential nesting success with distance from the forest edge (Angelstam 1986, Small and Hunter 1988, Yahner and Scott 1988, Robinson 1990, Filliater et al. 1994; see Paton 1994 for a critique). Nest success increased with distance from an edge when combining all nests located on our study sites (Hoover et al. 1995), but we did not detect an edge effect when we controlled for forest tract size in the logistic regression analysis. On small sites, predation rates were high throughout the forest and nest success was low. On large sites, predation rates were low throughout and nest success was high (Hoover et al. 1995). However, because most nests on small sites were near edges and most nests on large sites were away from edges, it is difficult to clearly distinguish between area and edge effects.

Nest predation is a major cause of nest failure for passerines as a group (e.g., Lack 1954; Ricklefs 1969; Martin 1992, 1993a) and for Wood Thrush specifically (Robinson 1992, Roth and Johnson 1993, Hoover et al. 1995, Robinson et al. 1995, Trine et al., 1998). The pervasive nature of nest predation and the potential influence of nest-site location on predation risk suggest that there should be strong selective pressure favoring individuals that choose nest sites that minimize the risk of predation (Martin 1992, 1993b). For Wood Thrushes nesting in highly fragmented landscapes, nest-site selection at the landscape level may be more important than at the level of the micro-habitat surrounding the nest. We

found that nesting success of Wood Thrushes increased, and conversely, that nest predation decreased with increasing size of forest tracts (Hoover et al. 1995). Also, the abundance or activity level of potential nest predators decreased with increasing size of forest tracts (Hoover et al. 1995). It appears that nest predation was influenced more by features of the landscape (area of forest, percentage of forest within a certain area; Hoover et al. 1995) than by specific characteristics of a nest site.

A combination of lower abundances of nest predators and lower rates of nest predation on large tracts of forest should favor Wood Thrushes selecting large tracts for nesting. Site fidelity has been found to be related to nesting success (Greenwood and Harvey 1982); and Roth and Johnson (1993) and Trine (in press) have found return rates to be higher for reproductively successful Wood Thrushes than for those that are not successful. High rates of nest predation in small tracts of forest may provide a partial explanation for the Wood Thrush being classified as "area sensitive" (Robbins et al. 1989, Askins et al. 1990). If predation rates remain high in small tracts of forest, over time we would expect the absence or rarity of Wood Thrushes and perhaps other migrants to become more rather than less pronounced on small tracts of forest. However, we do not expect to see a shift in nest-site selection within a forest tract because predation pressure probably is not consistent by predator type or over time, and nest predation could be nearly random.

Wood Thrushes appear to select certain structural components of the vegetation in the forest when establishing a breeding territory and follow some general behavioral "rules" (e.g., Best 1978, Morton et al. 1993, Filliater et al. 1994) when selecting a specific nest site within a breeding territory. For Wood Thrushes, simple behavioral rules for placing nests were to: (1) provide some concealment for the nest, (2) build the nest against or near the main stem of the vegetation supporting the nest, and (3) build the nest in tall (>2 m) shrubs if they are available. These rules apply to the nests that were built in our study area but may change in forests with different vegetation structure and species composition or in forests with markedly different nest predator communities. In regions where the nest predator community is diverse and habitat for nesting is not rare, it is probable that specific nest-site selection to avoid nest predation will not be favored and will not be apparent in studies of nest sites and nest predation. However, nesting in small tracts of forest, where both the abundance of potential nest predators and the rate of nest predation are high, should be selected against. This would result in nest-site selection to avoid predation being apparent at the level of the selection of a tract of forest rather than at the level of selection of specific nest-site characteristics within a tract of forest. As has been concluded previously (Hoover et al. 1995), the long-term health of Wood Thrush populations will depend on the maintenance of large tracts of forest.

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Notice

North American Loon Fund Grants

The North American Loon Fund (NALF) announces availability of 1999 grants in support of management, research, and educational projects directly related to the conservation of the family Gaviidae.

Proposals in the range of $500 to $3000 are most likely to be considered for funding. High priorities include projects designed to: 1) Identify and refine locations of important habitat areas for all loons during migration and winter, and for juvenile loons during summer. 2) Obtain more information on the population dynamics of all species of loons, including the average age of initial breeding, annual survival rate, longevity, and dispersal and sources of mortality. 3) Devise management methods to minimize the impact of pollution or human practices on loon populations, including direct practical techniques as well as techniques to assess the social and economic value of loons.

Deadline for submission of proposal is December 15, 1998. Funding awards will be announced by March 30, 1999. Please submit guideline request with S.A.S.E. to North American Loon Fund, 6 Lily Pond Rd., Gilford, NH 03246, U.S.A.

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PATTERN AND CHRONOLOGY OF PREBASIC MOLT FOR THE WOOD THRUSH AND ITS RELATION TO REPRODUCTION AND MIGRATION DEPARTURE

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ABSTRACT.—Documentation of the schedule and pattern of molt and their relation to reproduction and migration departure are important, but often neglected, areas of knowledge. We radio-tagged Wood Thrushes (*Hylocichla mustelina*), and monitored their movements and behavior on the U.S. Marine Corps Base, Quantico, Virginia (38° 40′ N, 77° 30′ W) from May–Oct. of 1993–1995. The molt period in adults extended from late July to early October. Molt of flight feathers lasted an average of 38 days (n = 17 birds) and there was no significant difference in duration between sexes. In 21 observed and captured individuals, all the rectrices were lost simultaneously or nearly so, and some individuals dropped several primaries over a few days. Extensive molt in Wood Thrushes apparently impaired flight efficiency, and birds at this stage were remarkably cautious and difficult to capture and observe. All breeding individuals were observed molting 1–4 days after fledgling independence or last-clutch predation, except for one pair that began molt while still caring for fledglings. Our data indicate that energetics or flight efficiency constraints may dictate a separation of molt and migration. We did not observe Wood Thrushes leaving the Marine Base before completion of flight-feather molt. Departure of individuals with molt in body and head, however, was common. We caution against interpreting the lack of observations or captures of molting individuals on breeding sites as evidence that birds actually have left the area. We argue also that current reports on overlapping of molt and migration based on observations of molting individuals out of the breeding range could be misleading because some individuals may leave the breeding area to molt in other places before starting a true migration. *Received 30 June 1997, accepted 18 March 1998.*

The Wood Thrush (*Hylocichla mustelina*) is one of the most studied avian species in North America, and details about its natural history are relatively well known (Roth et al. 1996 and citations therein). Despite this, information about its molt is limited and details on how molt is integrated with reproduction and migration departure are lacking. Separation of reproduction, molt, and migration within the annual cycle is considered an evolutionary strategy to reduce energetic stress (Payne 1972, Ginn and Melville 1983), but exceptions exist. Overlap of reproduction with flight- feather and extensive body molt is apparently common in tropical species (Payne 1972, Foster 1974). In temperate regions, its occurrence has been reported in some species that breed at high latitudes where food resources are abundant only briefly (Payne 1972). Joint occurrence of molt and migration is less common, except for species with a slow, diurnal migration with frequent feeding stops (e.g., hirundinids; Niles 1972).

The scarcity of information about timing and patterns of molt in Wood Thrushes and many other species is not unexpected. During the molt period, birds become secretive and less likely to be observed or caught, making documentation of activities during this period difficult (Ginn and Melville 1983). Because individuals of some species move away from their breeding territory for molting (Nolan 1978, Cherry 1985, Rappole and Ballard 1987) following these individuals can be difficult. Consequently, molt data often come from observations and/or recoveries of individuals of unknown breeding history or when known, these relationships have not yet been investigated. In recent years there has been an increased interest in use of radiotelemetry for the study of small birds, mainly because of the improvement in transmitter technology (i.e., smaller size). Transmitters are still relatively expensive and of limited range and life, but radiotelemetry-based studies can provide information that otherwise would be difficult to obtain.

The objectives of the study were (1) to provide information on the patterns and chronology of the prebasic molt in the Wood Thrush,

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and (2) to discuss the interaction between reproduction, molt, and migration departure.

For the Wood Thrush, a long-distance migrant of conservation concern (Hunter 1992), identification of the schedule of molt and its relation to reproduction and timing for migration are important for a better understanding of its biological cycle. Also, identification on how the molt process may modify the behavior of individuals and their vulnerability to predation may be critical to the conservation of this species.

STUDY AREA AND METHODS

The study was conducted at the U. S. Marine Corps Base in Quantico, Virginia, which is located 56 km southwest of Washington, D.C. on the eastern edge of the Piedmont Plateau physiographic region, along the west bank of the Potomac River (Hunt 1967). The Marine Base covers an area of 24,364 ha of which 75% is forested. The most common vegetation types included American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), oak (*Quercus spp.*) (47.5% of the forested area); Virginia pine (*Pinus virginianus,* 16.2%), and Virginia pine/oak (15.2%).

From May to October 1993–1995, we captured, radio-tagged, and monitored the movements and behavior of 42 juvenile and 61 adult Wood Thrushes as a part of a larger study on the behavioral ecology and habitat use of this species during the breeding and postbreeding periods (Vega Rivera 1997). During the breeding season, we captured and radio-tagged females and males positively identified as reproducing (i.e., those whose nests were found or who were associated with fledglings). Juveniles were captured during the nesting period by locating active nests, and during the postfledging period by mist-netting.

Because some adult birds were killed by predators, lost their transmitter, or left the study area before initiating molt, this analysis was based on observations of 30 radio-tagged individuals. Five of these birds were recaptured when molting. Additionally, we captured 13 molting adults for which we did not have previous data on reproductive activities. Information on juvenile molt was obtained from the capture of 23 molting individuals; 21 of these were captured after they had dispersed.

Adult and fledgling Wood Thrushes were fitted with radio transmitters attached using a backpack harness (Rappole and Tipton 1991). Each transmitter weighed 2.1 g (Holohil Systems Ltd., Woodlawn, Ontario, Canada) and made up 5–6% of the bird's body weight when attached. We detected no effect on the behavior of radio-tagged birds as compared with those without transmitters. Transmitters had an average life of at least 120 days, and could be detected at distances of 400–1000 m on the ground, and 1–3 km from the air.

Radio-tagged birds were located on foot on alternate days using a 4-element Yagi antenna and a 12-channel receiver (Telonics Communications, Inc.). When a bird's signal could not be found at its previous location, we searched first along roads using a 1-element antenna mounted on the roof of a truck. If loss of contact lasted more than 4 days, we also performed aerial radiotracking with a Cessna 172 at 350–500 m above ground in an area roughly 7 km in radius centered on a bird's last known location. We assumed that a bird had left the study area if we could not detect its signal during the aerial search. Signal loss also could have been due to transmitter failure, but our experience with these transmitters indicates that transmitter failure was rare.

For all captured individuals, we recorded the stage (old, missing, in pin, emerging, full grown/new) of remiges and rectrices and the condition of body molt. Additionally, in 8 of the 18 adults captured in molt, we recorded the length of flight feathers. Primaries, which number 10 in Wood Thrushes (10th vestigial, not considered), were numbered one to nine distally from the carpal joint. The secondaries were numbered one to nine from the carpal joint inward to the body, including the tertials S7–S9. The six rectrix pairs were numbered one to six distally from the center of the tail. Molt on four regions of the body was scored using the terminology of Niles (1972).

We pinpointed locations by approaching each bird until it moved. When possible, we made continuous observations on the bird's behavior up to 30 minutes after locating it. Specifically, we noted the type of activity (foraging or perching), substrate (ground, bush, tree), and interactions with conspecifics. Direct observation of radio-tagged birds allowed us to record if a bird was involved with breeding activities (either incubating, brooding nestlings, or caring for fledglings) or molting. To obtain data on onset of molt and date of departure from the study area, we relied on radiotracking data. Incipient molt was difficult to observe from a distance; therefore, for most birds we approximated the beginning of the molting period by backdating 15 days from the time we observed the birds in heavy molt. We based this approach on the observation that 13–16 days elapsed for four individuals captured before they started molting and later captured the first time they were observed in heavy molt. Additionally, for eight birds that changed locality after reproducing, a similar period elapsed between the day they moved to the new locality and the first day on which they were observed in heavy molt.

Throughout the paper, individual Wood Thrushes are referred to by a specific letter prefix followed by three numbers. The letter prefix refers to the individual's age/sex category: M = adult male, F = adult female, J = juvenile, and U = adult of unknown sex. Values presented are means ± SE. In all statistical tests a probability of 0.1 or less was accepted as significant. All statistical analyses were performed using SAS (version 6.03 for PC) software.

RESULTS

Most Wood Thrushes arrived at the study area in late April and early May. Nestlings

from first and second clutches fledged in late May–early June and late July–early August, respectively. For most pairs, timing of clutches subsequent to the first was associated with the success or failure of previous clutches. The latest record of an adult attending fledglings was 14 September, but most adults (90%) in the population completed their breeding activities by mid-August.

Of 61 adult birds radio tagged during the study, six birds were killed, seven lost their transmitters during nesting, and 18 (15 F and 3 M) left the study area after nest failure or fledgling independence. Of these, 13 females and 1 male left in June and early July, and 2 females and 2 males left in late July–August. Thirty (10 F and 20 M) adults stayed at the study area for molting. Of these, 11 (6 F and 5 M) molted in the same area where they nested; 4 males moved to deciduous sapling stands adjacent to their nesting territories and 15 (4 F and 11 M) moved 2015 ± 520 m (range 545–7291 m) from the mature deciduous or deciduous-pine forest where they had nested to Virginia pine forest, young deciduous stands, or forest edges where they molted.

Pattern of molt in adults.—A composite pattern of molt in adult Wood Thrushes is inferred from 18 captured individuals for which we recorded the molt stage. In eight of these birds, we measured remiges and rectrices (Fig. 1). None of these birds was recaptured, therefore we lack information on rate of growth.

Loss of P1 marked the beginning of molt in remiges. From there, molt proceeded sequentially, with P9 the last feather replaced. Similar size in adjacent growing remiges in five individuals suggested that replacement of these feathers may have occurred simultaneously or nearly so. In four individuals, molt of primaries in both wings showed some degree of asymmetry. Molt of secondaries S7–S9 (tertials) and S1–S6 was independent. Replacement of tertials apparently began at the same time as that of the inner primaries. The order of replacement of tertials varied, and was asymmetrical between wings for two birds. Molt of secondaries, S1–S6, started when replacement of the primaries was already underway; shedding of S1 occurred as P5 was out of the pin. Simultaneous replacement of two or three secondary feathers was observed in three individuals.

Twenty-one individuals lost all rectrices at once. They were observed without tail feathers or with growing rectrices of the same size. Shedding of the rectrices occurred shortly after P5 was replaced, and finished with the replacement of P9 or shortly after.

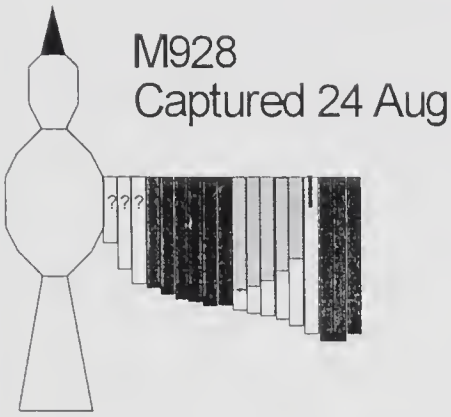
Body molt started before that of remiges and rectrices. Two males were captured showing body molt while still possessing all of their old flight feathers. By the onset of molt in remiges and rectrices, body molt was extensive, and continued at least 13 ± 1.4 days (n = 12) after molt of flight feathers was terminated or in its final growth stages. We base this statement on our observation of adults in full-new plumage still showing molt on the head the day before they left.

Molt chronology in adults.—The earliest record of a molting adult was of a male captured on 27 July with moderate molt on breast and sides. The earliest and latest records of adults observed having completed molt were 16 September and 14 October, respectively. For most adults, the molt period extended from early August to late September (Fig. 2). Mean date for onset of molt was 10 August (±2.1 days; females 15 August ± 3.4 days, n = 10; males 7 August ± 2.6 days, n = 17).

Molt of rectrices and remiges lasted 38.4 ± 0.7 days (n = 17) with no significant differences (t-test, $t = -0.90$, $P > 0.10$) between males (38.9 ± 0.8 d; n = 11) and females (37.5 ± 1.6 d; n = 6) . Complete molt lasted 52.0 ± 1.1 days (n = 21), and was longer (t-test: $t = -1.80$, $P < 0.10$) in males (53.2 ± 1.1 days, n = 15) than females (49.2 ± 2.3 days; n = 6). Our data suggest that Wood Thrushes that started molting earlier in the season extended the molt over a longer period (Pearson correlation: $r = -0.83$, $P < 0.001$; n = 21; Fig. 3).

→

FIG. 1. Molt stage of adult Wood Thrushes captured Aug.–Oct. 1995–1996 in Quantico, Virginia. Dark bars represent old feathers; light-grey bars represent new full-grown and partially growing feathers; narrow-dark bars represent pin feathers. Birds with one wing had symmetrical molt. All birds had heavy feather growth on body.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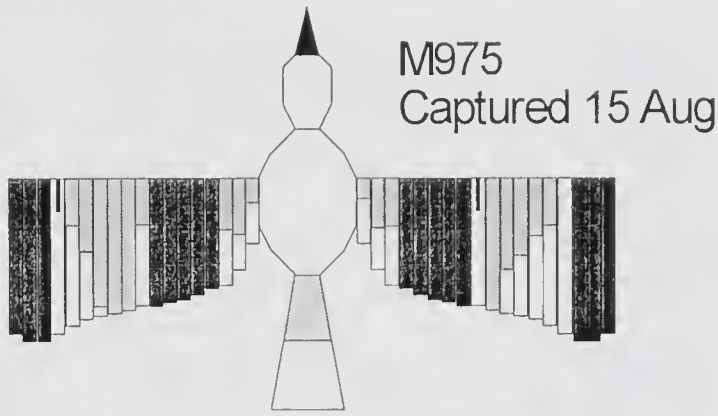
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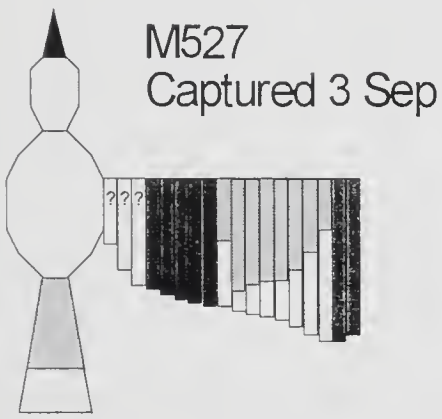
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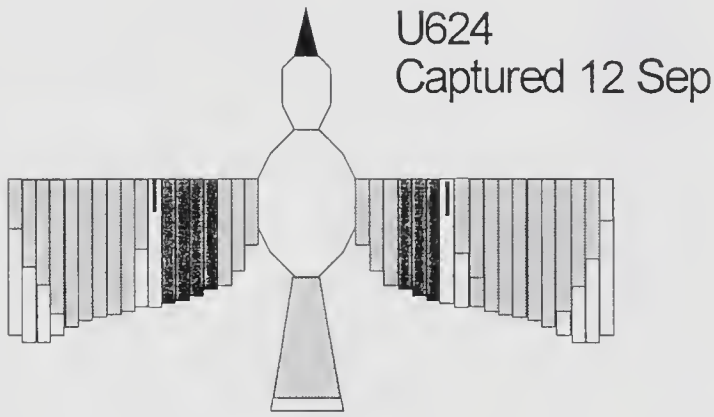
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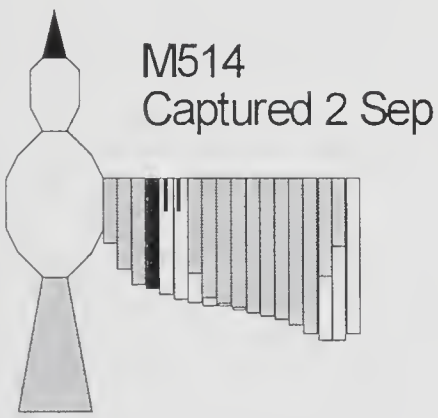
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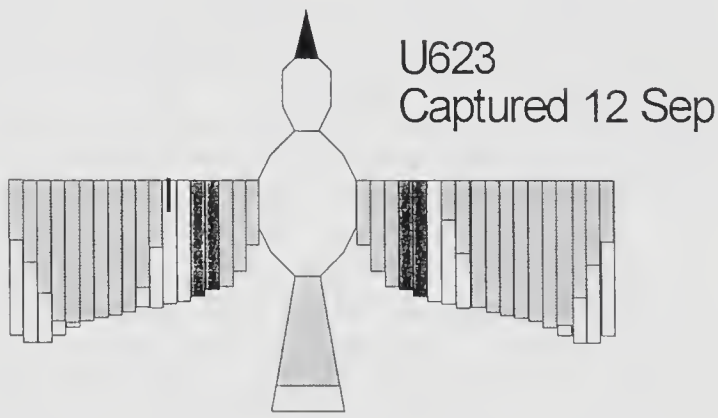
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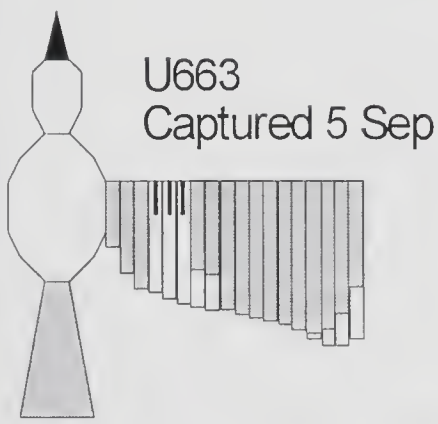
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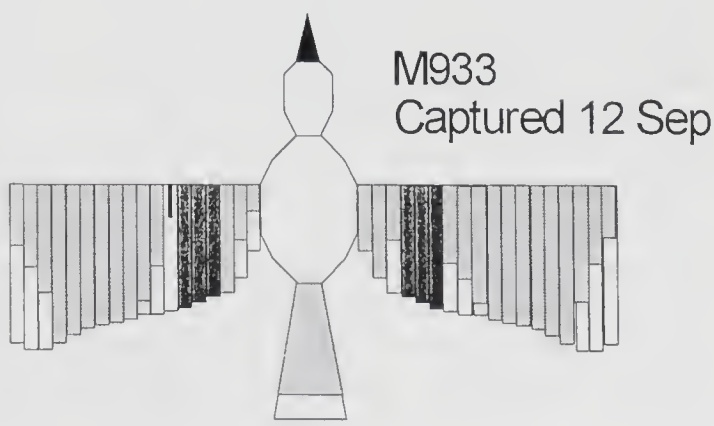
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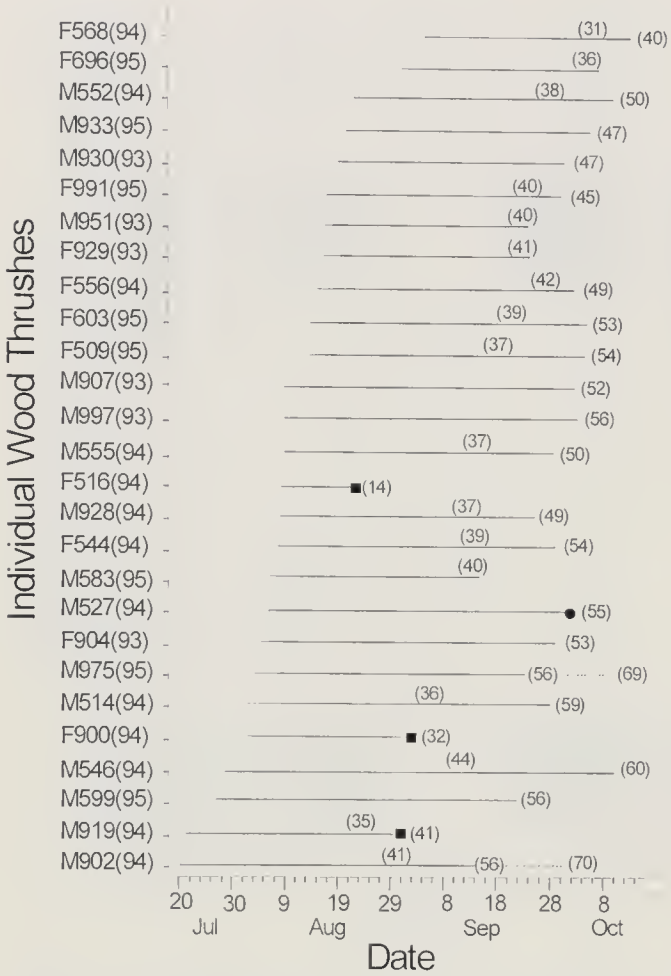

FIG. 2. Molt chronology in adult Wood Thrushes breeding in Quantico, Virginia. Numbers above and at the end of the lines indicate the duration (days) of flight-feather and complete molt, respectively. A dotted line represents a bird staying in the molting area after the end of the molt. A circle indicates that the transmitter fell off the bird. A square indicates that the bird was killed.

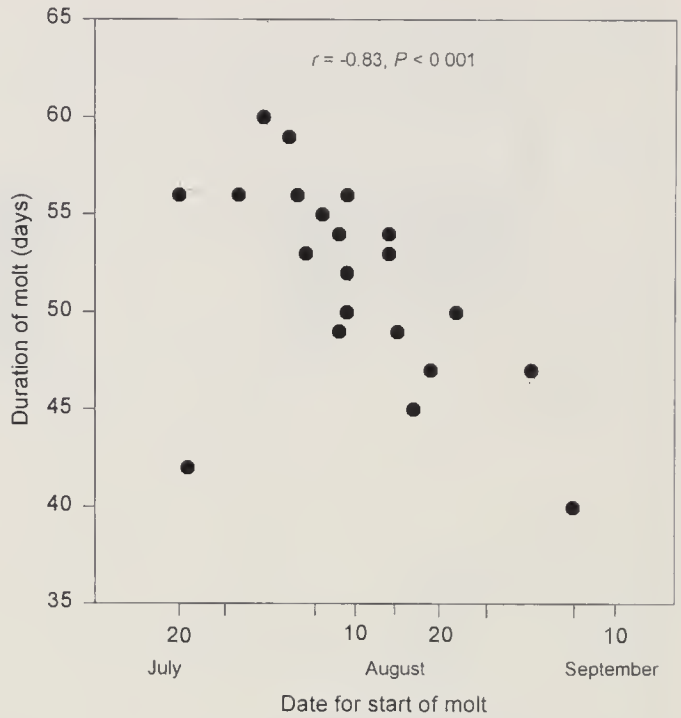

FIG. 3. Correlation between duration of molt (20 July = day 1) and date of onset of molt in adult Wood Thrushes (Pearson Correlation Coefficient; $r = -0.83$, $P < 0.001$).

Adult behavior during molt.—According to our observations of radio-tagged adults, heavy molt seriously impaired maneuverability and ability to sustain flight. We observed five individuals that for at least 10 days could barely fly. For instance, while we tracked a molting female, she was observed to hop 1 m up a branch from which she attempted to fly but could not. She fell to the ground, and disappeared, hopping and flapping her wings. Molting adult Wood Thrushes, at least during the heaviest molt stage, were very difficult to observe, and almost impossible to capture in mist nets. They hid on the ground in the densest patches of vegetation where, on occasions, we had to approach within 3 m to make them move, and ensure that they were alive. These behavioral changes were also evident when we compared the mean distance between consecutive radiolocations in nesting versus molting sites for 23 birds (114 ± 9 m and 67 ± 8 m, respectively; Wilcoxon test: $Z = 3.13$, $P = 0.002$) and size of the area used (95% convex polygon, 2.6 ± 0.5 ha and 1.4 ± 0.3 ha, respectively; $Z = 1.88$, $P < 0.1$).

Overlap between reproduction and molt.—For molting birds for which we obtained breeding data, molt was initiated after reproduction was completed. For these birds, molt began 1–4 days after their young reached independence or after nest failure. We observed only one pair caring for fledglings while molting. This pair was captured when we radio-tagged their three nestlings, on 22 August. The male had general, light body molt. On 6 September, while still caring for one fledgling, the male had lost his rectrices and showed heavy general body molt. It was not until seven days later that the fledglings became independent. The female attended two of the three fledglings. At the time of capture she was not molting. On 14 September, while still caring for one fledgling, she was in heavy general body molt. Next day the fledgling had dispersed, and the female was without rectrices.

Overlap between molt and migration de-

parture.—Twenty-three of 30 birds that bred and molted at the study area, and for which we had data, left between 15 September and 14 October. All of these birds had completed flight feather molt by the time they left. Five individuals were known to still have head molt in progress on the day before they left.

Prebasic molt in juveniles.—We captured 23 juvenile Wood Thrushes in moderate to heavy general body molt. The earliest date on which a juvenile in molt was captured was 27 July. This was an individual with incompletely grown rectrices and light molt on the sides. Nine more juveniles were captured from 9–20 August and 12 from 2–5 September. The last date on which a molting juvenile was captured was 18 September. Juveniles left the study area in September and early October, with 47% leaving in September.

DISCUSSION

Molt in adults.—The replacement of remiges in Wood Thrushes, including the tertiaries which were molted ahead of the other secondaries, was typically passerine (Dwight 1900). Simultaneous molt of rectrices, which occurred routinely in our population, is not a common pattern in passerines (Pyle et al. 1987). In Wood Thrushes, its occurrence was previously reported by Weaver (1949). Roth and coworkers (1996) reported 3 adults that dropped all rectrices at once. The only other member of the Turdiniae for which data are available is Swainson's Thrushes (*Catharus ustulatus;* Cherry 1985). Based on calculation from recaptured individuals, this species required 32 days to complete flight-feather molt, which is close to the measure reported here for the Wood Thrush (38 days).

Sex differences in molt.—Our data suggest that adult male Wood Thrushes commenced molt prior to adult females. Average date of onset of molt in males was eight days earlier than for females. These results agree with numerous reports for other passerine species (e.g., Verbeek 1973, Rimmer 1988, Norman 1990). In our population, the difference in onset of molt between the sexes could have been influenced by female dispersal. In this study, 15 females, but only 3 males that bred at the study area, left before molting. Thus, we did not get information on when those females started molting. Our observations of molting individuals for which we had information on breeding activities suggest that emancipation from parental care by one parent corresponded to initiation in molt in that parent. This observation agrees with published information from studies of other passerine species where known breeding pairs have been identified (e.g., Morton and Welton 1973, Sealy 1979, Tiainen 1981).

Behavior during molt.—Flight efficiency in adult Wood Thrushes was reduced during extensive molt. Twenty-one birds on which we had observations lost all rectrices at once and five lost several primaries over a short time. Simultaneous replacement of flight feathers in waterfowl, resulting in temporary flightlessness, is well known (Jehl 1990). In passerines, there are scattered reports that extensive molt may impair or even prevent flight (e.g., Haukioja 1971, Verbeek 1973, Rimmer 1988). Haukioja (1971) suggested that this condition in passerines is probably more common than has been estimated from captures or visual observations, but furtive behavior associated with this condition made its detection difficult.

Lack of observations or captures of molting individuals on their nesting sites have been used as justification for the conclusion that birds actually have left the nesting area (for instance Sealy 1979). We caution against this interpretation. In this study, if molting birds had not been radio-tagged, they would likely have passed unnoticed because they were furtive, silent, and flew very little. Capturing radio-tagged molting Wood Thrushes using passive mist netting was difficult. On several occasions, we surrounded molting birds with mist-nets and yet failed to capture them. Only active chasing of the birds toward the nets proved to be effective.

Reduced ability to fly may result in increased predation, but during this study only two radio-tagged adults were predated while molting, whereas six were predated when they were nesting. Survival during extensive molt can be enhanced by behavioral inconspicuousness and/or selection of safe areas (Jehl 1990). Both strategies apparently were adopted by molting Wood Thrushes; they were secretive and they molted in sites with vegetation attributes, such as a dense understory, that may have enhanced protection (Vega Rivera 1997).

Relation between reproduction and molt.—Separation of breeding and molt is considered a general strategy that allows these processes to occur with minimal nutritional stress (Payne 1972, Morton and Welton 1973, Ginn and Melville 1983; but see King and Murphy 1985, Murphy 1996). The initiation of molt while still caring for fledglings has been reported for several species (e.g., Rimmer 1988, Norman 1990, Zaias and Breitwisch 1990, Evans Ogden and Stutchbury 1996). In our study, all known breeding Wood Thrushes apparently began molt after their young reached independence or after nest failure, but two individuals were found molting while caring for fledglings.

It is possible that more Wood Thrushes started molting while still taking care of fledglings, but we lack documentation because of our inability to detect incipient body molt without actually capturing the bird. When we recorded a bird as molting based on observations only, it was the "notable molt" of Nolan (1978) that we recorded, i.e., a bird with heavy molt on the head or with missing/growing flight feathers. None of the birds in this condition, with exception of the two birds mentioned, were in the company of fledglings.

In our radio-tagged population, reproductive effort was apparently extended to a point where it did not compromise the timing of molt and migration. Reproduction, from building of the nest to fledgling independence, took about 51 days. Molt of flight feathers took an average 38 days. If we consider that 91% of the adults left the study area between 22 September–10 October, then the latest any pair should have initiated a clutch was 25 June–13 July. These dates agree with our data. Except for one pair, which began nest building on 22 July, all breeding pairs initiated their last clutch before 13 July.

An overlap between care of fledglings and onset of molt would effectively prolong the potential reproductive period for an individual (Foster 1974, Evans Ogden and Stutchbury 1996). We suggest that Wood Thrushes attending the last brood of the season may initiate molt a few days before fledgling independence with minimal nutritional stress for two reasons. First, close to independence, Wood Thrush fledglings feed mostly by themselves; therefore their demands for food from parents probably are low. Also, at this time fledglings are capable of full flight and thus they are less vulnerable to predators which makes parental role in this aspect less critical (Vega Rivera 1997). Second, at the study area the onset of adult molt coincided with a time when production of fruits and berries was high. Based on our observations as well as information in the literature (Martin et al. 1951, Conway et al. 1994, Roth et al. 1996), these resources are commonly eaten by Wood Thrushes in late summer and fall.

Relation between molt and migration.—Simultaneous occurrence of flight feather or extensive body molt and migration is considered incompatible because of the negative effects on flight efficiency and nutritional condition (Kjellén 1994). Indeed, for most species it is assumed that molt is scheduled so that migrant birds have fully functional flight feathers at the time of migration (Ginn and Melville 1983). Based on our observations, we have no evidence that Wood Thrushes molting at the study area left before the replacement of remiges and rectrices was complete. Departure with light body molt was not uncommon.

There are, however, reports that individuals of some species migrate while molting (e.g., Hyytiä and Vikberg 1973, Sealy 1979). We suggest that many records of birds showing flight feather or heavy body molt found outside the breeding range may represent relocation to special molting sites rather than migration. Rappole and Ballard (1987) proposed that birds of many species may move to special molting areas safer from predators and/or with better food resources than nesting habitats. Cherry (1985) captured molting Swainson's Thrushes 30, 150, and 250 km from the closest known breeding areas for the species. He concluded that Swainson's Thrushes are unlikely to initiate actual southward migratory movement during the middle of molt. In our study, 18 adults left the study area after nest failure or fledgling independence. These birds were probably not migrating, but were moving elsewhere to renest or initiate molt. We base this conclusion on the fact that intensive study of this species documents that transients do not arrive in south Texas until late to mid-September (Rappole and Blacklock 1995) or in Veracruz, Mexico, until early October (Winker et al. 1990).

We propose that birds that left the study area relocated some distance from their nesting sites to specific molting areas. They remained for several weeks in these areas while completing molt and preparing for migration, following a time sequence very similar to the birds that remained on the study area. Testing of this hypothesis will require additional studies.

ACKNOWLEDGMENTS

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SEASONAL CHANGE OF FLOWER USE BY THE SLATY FLOWERPIERCER (*DIGLOSSA PLUMBEA*)

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ABSTRACT.—I observed a pair of Slaty Flowerpiercers (*Diglossa plumbea*) in highland Costa Rica during 1996 and quantified their flower use in three distinct months. The total number of open flowers in the territory declined from dry to wet season, and the composition of flower species changed. The pair changed their flower use from dry to wet season, exploiting more abundant flower species in each season. Previous studies have shown that the change of flower abundance and composition affected hummingbird abundance in this area because they leave the area when their favorite flower species become scarcer. The Slaty Flowerpiercers, in contrast, maintained the same territory, shifting flower use in response to seasonal changes in flower abundance and composition. My observations suggest that the unique feeding method of flowerpiercers as "nectar thieves" allows them to use flowers more flexibly and to remain resident on the same territory throughout the year.
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The Slaty Flowerpiercer (*Diglossa plumbea*) is a small, nectarivorous passerine endemic to the highlands of Costa Rica and western Panama (A.O.U. 1983, Sibley and Monroe 1990, Hackett 1995). It is usually found at forest edges and gaps, and shrubby clearings, where flowering plants are abundant (Ridgely 1989, Stiles and Skutch 1989). Flowerpiercers have been considered to be nectar thieves rather than legitimate pollinators, because they pierce and extract nectar from the base of the corolla without pollinating [Skutch 1954, Moynihan 1963; however, Graves (1982) reported pollination of *Tristerix longebracteatus* (Loranthaceae) by *Diglossa brunneiventris* and *D. humeralis* in Peru].

A nectarivorous bird community in highland southern Costa Rica has been studied in detail because of its simplicity (Wolf 1969, Wolf and Stiles 1970, Colwell 1973, Wolf et al. 1976). Most of these studies have focused on hummingbirds, and the Slaty Flowerpiercer has been mentioned only as a "parasite" of this hummingbird community (Colwell 1973, Colwell et al. 1974, Wolf et al. 1976); use of flowers by the flowerpiercer has not been quantified. The ecology of the Slaty Flowerpiercer differs from that of hummingbirds in two ways suggesting that its flower use differs from that of hummingbirds: the absence of coevolution with flower species because of the presumed lack of pollination, and little restriction in flower use because of its unique feeding method.

STUDY AREA AND METHODS

I observed a marked pair of Slaty Flowerpiercers on the Cerro de la Muerte, prov. San José, Costa Rica (09° 33′ N, 83° 43′ W). I visited the area at least once a month throughout 1996 and quantified their flower use in three months: January, February and August. The dry season of this area starts in December and lasts until April (average rainfall less than 100 mm/month); the other months receive relatively high precipitation (average rainfall 200–500 mm/month; Wolf 1976). In January, the pair had two fledglings whom they actively fed with nectar and insects. I considered that these three months would represent three different conditions under which the Slaty Flowerpiercers might behave differently: dry and breeding (January), dry and non-breeding (February), and wet and non-breeding (August). The study area is composed of shrubby secondary growth along a local road used for maintenance of electric towers, but behind the second growth is montane oak forest. The observed pair maintained the territory of 150 × 40 m throughout the study. The territory was delimited on the north and south sides by the secondary oak forest, and defended on the east and west sides against other marked conspecific pairs. The territory boundary as delineated by movements of the marked individuals and agonistic interaction with neighbors stayed unchanged during my observations. To quantify flower use, I followed each individual as long as possible and counted the number of visits to each flowering shrub that I had previously marked and identified. I observed each member of the pair for 24–26 hours in each month; total 150 hours for three months. The number of all the open flowers in the territory was counted in each month. I used the nectar concentrations and production rates of flower species that appeared in Wolf and coworkers (1976), but also

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TABLE 1. Number of open flowers found in the territory of one pair of Slaty Flowerpiercers on the Cerro de la Muerte, Costa Rica, in 1996.

Family	Flower species	Month			Nectar production (J/h)
		Jan	Feb	Aug	
Polygalaceae	*Monnina xalapensis*	5945	4519	563	1.88
Campanulaceae	*Centropogon valerii*	364	534	95	9.94[a]
	C. costaricae	331	460	391	4.85
	C. talamancensis	191	168	361	8.89[a]
Ericaceae	*Macleania rupestris*	7	54	318	<1.74[a]
	Cavendishia craciffolia	6	0	206	11.47
	Gaultheria erecta	—	1036	18	1.05–1.39[a]
Onagraceae	*Fuchsia microphylla*	428	511	149	0.70–1.05[a]
Scrophulariaceae	*Digitalis purpurea*	0	0	39	—
Loranthaceae	*Gaiadendron punctatum*	400	20	0	2.79[a]
Alstroemeriaceae	*Bomarea* sp.	52	191	—	—
Rosaceae	*Rubus* sp.	15	—	—	1.39–1.74[a]
	Total	7739	7493	2140	

[a] Values are from Wolf and coworkers (1976).

measured some additional species (see Table 1). All the statistical tests employed SYSTAT (Wilkinson 1990) except the analyses of frequencies; likelihood ratio G-test and G-test of independence to analyze the seasonal change of flower abundance; flower composition, and flower use were performed following Sokal and Rohlf (1995).

RESULTS AND DISCUSSION

Change of flower abundance.—The number of open flowers in the territory changed drastically from dry season (January and February) to wet season (August; likelihood ratio test: G = 3935, 2 df, $P < 0.001$; Table 1). The composition of flower species also changed from dry to wet season (test of independence: G = 4296, 16 df, $P < 0.001$; Table 1). In the dry season, *M. xalapensis* represented 60–77% of all open flowers. *Fuchsia microphylla, Centropogon valerii,* and *Centropogon costaricae* followed this species in abundance, with 396–470 open flowers each (each 5–6% of all flowers). From dry to wet season, *M. xalapensis, F. microphylla,* and *C. valerii* declined in abundance, while two species of Ericaceae, *Macleania rupestris* and *Cavendishia craciffolia* increased. In the wet season, *M. xalapensis* still represented 26% of all open flowers, although the number decreased by 90% from the dry season. *Centropogon costaricae, Centropogon talamancensis, M. rupestris,* and *Cavendishia craciffolia* followed in abundance with 206–391 open flowers each (each 10–18% of all flowers).

Change of flower use.—The male and the female changed their flower use in similar ways (Fig. 1). In the dry season, *C. valerii* and *M. xalapensis* were visited most frequently by both the male and the female (58.2–71.7 % of all visits, combined). In the wet season, use of these flowers declined significantly (Test of independence using sum of *C. valerii* and *M. xalapensis* against the rest of flower species; male: G = 74; female: G = 87; both: 2 df, $P < 0.001$) with their decrease in availability, and two other flower species became important in their diet (24.2–25.8 % of all visits, combined): *M. rupestris* and *C. craciffolia,* both of which had few flowers in the dry season but flowered abundantly in the wet season (Table 1). These changes of flower use coincide with the changes of each flower species in abundance.

The flower abundance of each species varied in a different way over the year, thus changing the overall species composition and the number of available flowers (Table 1). Previous studies have shown that seasonal change in flower abundance and composition affect abundance of four hummingbird species found in the area (Wolf et al. 1976). Hummingbirds have evolved bill morphology and body size consistent with a particular set of flowers (Colwell 1973, Wolf et al. 1976), and thus they leave the area when their favorite flowers decrease in abundance (Wolf 1969, Colwell 1973, Wolf et al. 1976). These changes in

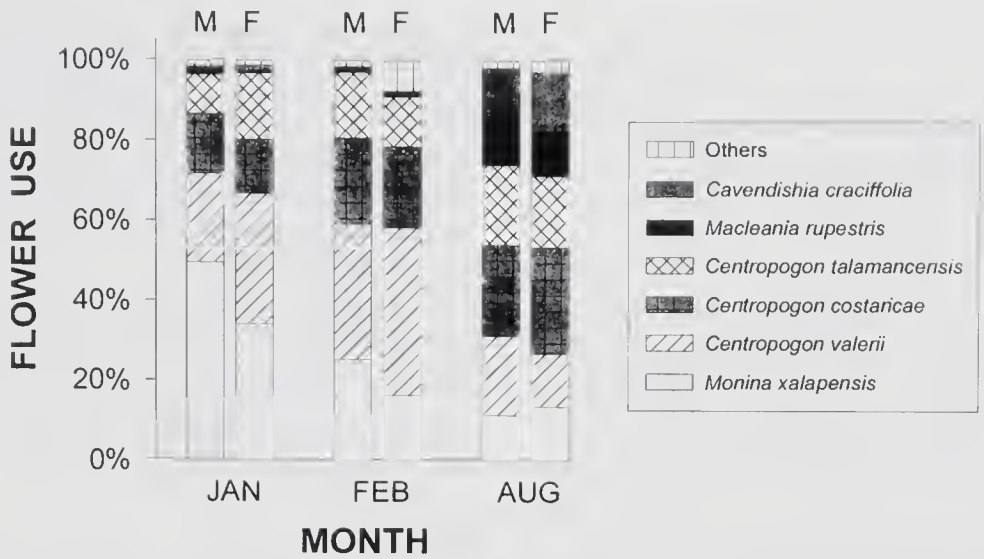

FIG. 1. Seasonal change of flower use of the male and female Slaty Flowerpiercers (*Diglossa plumbea*) on the Cerro de la Muerte, Costa Rica, in 1996. (male: n = 374 in January, n = 500 in February, n = 147 in August; female: n = 147 in January, n = 357 in February, n = 265 in August)

flower abundance and composition do not appear to cause seasonal movement in Slaty Flowerpiercers, which remained on the same territory throughout the year, adjusting their diet to the changing resource. Presumably, the lack of coevolution with certain flower species and its unique foraging method permit the Slaty Flowerpiercer to use flowers more flexibly than hummingbirds.

Flower preference.—To measure flower preference, I used the forage ratio: the quotient of the proportion of flower use divided by the proportion of flower abundance (Krebs 1989:393). If the Slaty Flowerpiercer did not demonstrate preference for certain flowers and used all flower species proportionally to their availability, then the forage ratios should be nearly one. The forage ratios of 7 flower species revealed a striking difference in preference among flower species (Table 2; Friedman's test, male: F = 10.7; female: F = 11.5; both: 4 df, $P < 0.05$). The male and female demonstrated very similar forage ratios for each flower species (Spearman's rank correlation: r_s = 0.87, n = 28, $P < 0.001$). The forage ratios did not change significantly among months (Friedman's test, male: F = 3.9; female: F = 3.1; both: 2 df, $P > 0.05$). *Centropogon valerii* was the most preferred flower species for both sexes in all three

TABLE 2. Forage ratio for twelve flower species for the male and female Slaty Flowerpiercers on the Cerro de la Muerte, Costa Rica, in 1996.[a]

Flower species	Male				Female			
	Jan	Feb	Aug	$\bar{x}$ ±SD	Jan	Feb	Aug	$\bar{x}$ ±SD
Monnina xalapensis	0.64	0.41	0.43	0.49 ±0.13	0.44	0.27	0.52	0.41 ±0.13
Centropogon valerii	4.68	4.65	4.48	4.60 ±0.11	6.88	5.90	3.06	5.28 ±1.98
C. costaricae	3.47	3.41	1.25	2.71 ±1.27	3.15	3.31	1.48	2.65 ±1.02
C. talamancensis	3.87	7.04	1.18	4.03 ±2.94	6.56	5.48	1.07	4.37 ±2.91
Macleania rupestris	—	—	0.82	0.82	—	—	0.77	0.77
Cavendishia craciffolia	—	—	1.24	1.24	—	—	1.53	1.53
Gaultheria erecta	—	0.04	—	0.04	—	0.22	—	0.22
Fuchsia microphylla	0.10	0.06	0.10	0.08 ±0.02	0.24	0.24	0.00	0.16 ±0.14
Digitalis purpurea	—	—	0.73	0.73	—	—	0.00	0.00
Gaiadendron punctatum	0.21	—	—	0.21	0.00	—	—	0.00
Bomarea sp.	0.00	0.00	—	0.00	0.00	0.00	—	0.00
Rubus sp.	0.00	—	—	0.00	0.00	—	—	0.00

[a] Forage ratios differed among flower species (Friedman's test, male: F = 10.7; female: F = 11.5; both: 4 df, $P < 0.05$), but not among months (Friedman's test with five flower species which had data for all three months, male: F = 3.9; female: F = 3.1; both: 2 df, $P > 0.05$).

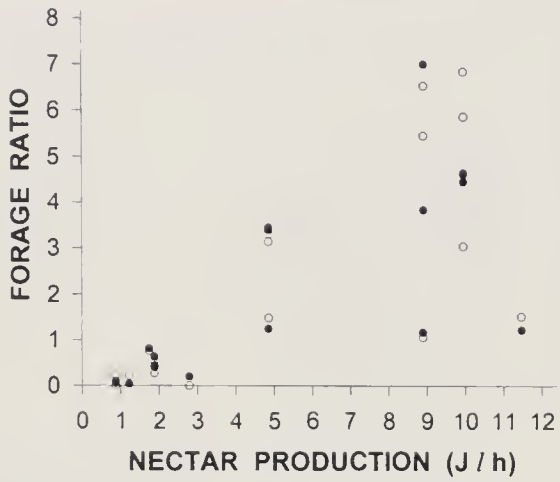

FIG. 2. Flower preference of the Slaty Flowerpiercer (*Diglossa plumbea*): forage ratio versus nectar production for each flower species on the Cerro de la Muerte, Costa Rica, in 1996. (●: male, ○: female; Spearman's rank correlation: $r_s = 0.82$, $n = 38$, $P < 0.001$)

months except February when the male preferred *C. talamancensis* (Table 2). The forage ratios were positively correlated with calorie production rates of each flower species (Spearman's rank correlation: $r_s = 0.82$, n = 38, $P < 0.001$; Fig. 2).

It is not surprising that the forage ratios for each flower species did not differ between two Slaty Flowerpiercers and were not affected by flower abundance. To maximize foraging efficiency, they chose some nectar rich flower species from the wide range of available flower species. I have not considered other factors that could also affect the forage ratio, such as the distance to the nearest flower patches, the number of flowers available per flower patch, and intensity of interaction with competitors (Wolf et al. 1975, Gill and Wolf 1979). Interaction with more aggressive, territorial hummingbirds such as the Fiery-throated Hummingbird (*Panterpe insignis*) or the Green Violet-ear (*Colibri thalassinus*) could decrease the foraging efficiency of the Slaty Flowerpiercer, because these hummingbirds defend the flower patch against the Slaty Flowerpiercer (Lyon and Chadek 1971, Colwell et al. 1974, pers. obs.). In August, Fiery-throated Hummingbirds were numerous in the study area and the surroundings; they established territories around the shrubs of *C. craciffolia* and *M. rupestris*. The interaction between the Slaty Flowerpiercer and the hummingbirds, measured by the frequency of physical attacks and approach per unit time, increased drastically during August compared to January and February when few Fiery-throated Hummingbirds were in the study area (Naoki, unpubl. data). Perhaps this explains why the forage ratio for *C. craciffolia* is low despite its high nectar production.

In summary, this pair of the Slaty Flowerpiercers shifted their foraging in response to seasonal changes in flower abundance and composition. Because my data set is based on one pair of birds and on one year, conclusions are necessarily tentative. Nevertheless, these data suggest that the morphological and behavioral adaptations of flowerpiercers which allow them to use almost any flowers also allow them to remain resident on the same territory through the year, unlike pollinating hummingbirds which move seasonally in response to flower availability.

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PROVISIONING OF NESTLINGS BY MALE AND FEMALE YELLOW-BREASTED CHATS

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ABSTRACT.—Observations of parental feeding roles were made at 19 Yellow-breasted Chat (*Icteria virens*) nests during the 1994 breeding season in central Kentucky. Male and female chats fed nestlings at similar rates, and adult feeding rates were unaffected by brood size. The absence of any change in feeding rates with increased brood size suggests that food requirements per nestling decrease as brood size increases, perhaps because of differences in thermoregulatory costs. In contrast to the results of many other studies, provisioning rates and load sizes (number of prey delivered per visit) did not increase with nestling age. However, our observations at chat nests did not begin until nestlings were 3 or 4 days old. Studies of other species have revealed that 1–3 day old nestlings may be visited less frequently and provided with smaller loads than older nestlings, and observations of nestling chats during this early period might have revealed similar behavior. *Received 2 Aug. 1996, accepted 30 April 1998.*

Among altricial birds, the behavior of parents providing food for nestlings may be influenced by several factors. For example, differences in brood size and nestling age may contribute to changes in feeding rates or the size and type of prey delivered to nestlings. However, previous work has revealed interspecific differences in how parents respond to changes in these and other factors. For example, adult Bachman's Sparrows (*Aimophila aestivalis*) make more feeding visits to large broods than to small broods (Haggerty 1992), but adult Field Sparrows (*Spizella pusilla*) do not (Best 1977). Previous studies have also revealed interspecific differences in the respective roles of males and females in provisioning nestlings. In some species, males and females provision nestlings at similar rates [e.g., Northern Mockingbird (*Mimus polyglottos*), Breitwisch et al. 1986] while, in other species, either males [e.g., Gray Catbird (*Dumetella carolinensis*), Johnson and Best 1982] or females [e.g., Eastern Bluebird (*Sialia sialis*), Pinkowski 1978] may deliver food at higher rates. The reasons for such interspecific variation in parental provisioning behavior remain unclear. Additional studies can help elucidate those factors contributing to such interspecific variation (Haggerty 1992).

Most Yellow-breasted Chats (*Icteria virens*) are socially monogamous (Thompson and Nolan 1973; Schadd and Ritchison, pers. observ.) and, at least in the southern parts of their range, double-brooded. Males arrive on the breeding grounds several days before the females. Chats generally build nests 0.6–1.8 m above the ground in dense vegetation (Harrison 1975). Females typically lay three to five eggs and the incubation period is about 11 days (Bent 1953, Harrison 1975). Young fledge 8–11 days after hatching (Bent 1953; Schadd and Ritchison, pers. obs.). Currently, little is known about the parental behavior of Yellow-breasted Chats. The objectives of our study were to (1) quantify the parental behavior of adult chats, (2) compare the roles of males and females in caring for nestlings, and (3) examine the effects of brood size and nestling age on parental provisioning behavior.

STUDY AREA AND METHODS

Chats were studied at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison Co., Kentucky. Beginning in late April 1994, male chats were captured by placing mist nets in known territories or by luring them into mist nets using playback of chat songs. Females were captured by placing mist nets in known territories or, later in the season, by placing mist nets near nests. Captured chats were banded with a numbered aluminum band plus a unique combination of colored leg bands. Beginning in early May, females were monitored for signs of nesting, such as carrying nesting material. If not located during nest building, nests were located by observing the behavior of adults or by checking likely nest sites.

From 3 June through 26 July 1994, observations of adults and nestlings were made at 19 nests using camcorders. To ensure that adults would not abandon nests, videotaping at nests did not begin until nestlings were at least 3 days old. Observation periods (i.e., taping

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sessions) were 2–6 hours in duration, with most taping conducted during the period from 06:00 to 12:00.

For each parental visit to a nest, we determined the sex of the parent using either the amount of black on the bill [males typically have completely black bills while females have varying amounts of gray in their bills (Ritchison, unpubl. data)] or the colored leg bands. We also noted the number, size, and type (adult or larval insect) of prey brought to the nest. Prey sizes were categorized as small (less than or equal to the length of the parent's beak), medium (greater than the length of the parent's beak to twice that length), or large (greater than twice the parent's beak length).

Because multiple observations were made of each nest, we used repeated measures ANOVA (Beal and Khamis 1990). To examine possible differences in the sizes of prey delivered to broods of different sizes or nestlings of different ages, analyses were conducted using weighted sums. For each observation period, we determined the number of prey in each size category (small, medium, and large) delivered by adults and then multiplied the number of small prey delivered by one, the number of medium prey by two, and the number of large prey by three. The sum of these products was divided by total observation time and the resulting rates were then subjected to analysis. Possible variation in the types of prey fed to nestlings (adult insects versus larvae) was examined using the ratio of adult to larval insects delivered during each observation period. All statistical analyses were conducted using the Statistical Analysis System (SAS Institute 1989). All values are presented as mean ± one standard error.

RESULTS

Each chat nest (n = 19) was videotaped over an average of 3.2 days. Overall, these nests were videotaped for 260 h ($\bar{x}$ = 13.7 h/nest; range = 4–24 h/nest), and during this time adult chats made 711 feeding visits ($\bar{x}$ = 37.4 visits/nest; range = 11–69). At 14 nests, both adults fed the young, while at five nests, only one adult fed the nestlings. At four of these nests ($\bar{x}$ = 14.3 hours of videotaping/nest), the male made all recorded visits, while the female made all recorded visits at one nest (24 hours of videotaping).

Young fledged from 16 of 19 chat nests (84.2%). The mean number of young fledged from successful nests was 3.25 ± 0.17. Nests at which both parents were observed feeding nestlings fledged more (z = 2.16, P = 0.031) young ($\bar{x}$ = 3.14 ± 0.29) than did nests where only one adult was observed feeding nestlings ($\bar{x}$ = 1.52 ± 0.68). Young fledged at 13 of 14 nests with both parents providing care and at 3 of 5 nests where only one parent was observed providing care, and this difference was not significant (Fisher's exact test: $P > 0.05$). Nestlings at all three unsuccessful nests appeared to be healthy and were apparently lost to predators [a black rat snake (*Elaphe obsoleta*) was video-taped preying upon nestlings at one of these nests].

Adult chats delivered food to nestlings an average of 2.56 ± 0.16 times/h (n = 62 observation periods). After arrival at a nest, the mean time until adults fed a nestling was 3.69 ± 0.27 sec (n = 701). The mean number of prey items brought to nests by adults during each visit was 1.52 ± 0.02 (n = 711 visits), and adults never brought more than three items. The most common prey size was medium (56.8% or n = 602 of 1061). Small prey accounted for 15.8% (n = 168) of prey items, and large prey 27.4% (n = 291). Most prey brought to the nest were adult insects (n = 601 or 56.7%), while 43.3% (n = 459) were larval insects.

Only female chats brooded nestlings, and the frequency of brooding by females declined with increasing nestling age. Females brooded 3 and 4 day old nestlings during 45% of all nest visits (n = 88), and this frequency declined to 22% for 5 and 6 day old nestlings (n = 129) and 21% for 7 and 8 day old nestlings (n = 120).

Males vs females.—We found no differences ($F_{1,18}$ = 0.7, $P > 0.05$) between the feeding rates of females ($\bar{x}$ = 1.24 ± 0.14 feedings/h; n = 62 observation periods) and males ($\bar{x}$ = 1.32 ± 0.12 feedings/h). Similarly, males and females did not differ in the mean number of prey brought to the nest per visit ($F_{1,14}$ = 0.0, $P > 0.05$), with males averaging 1.50 ± 0.03 (n = 373) and females 1.54 ± 0.03 (n = 338) prey per visit. We also found no difference in the size of prey delivered by males and females ($F_{1,18}$ = 0.32, $P > 0.05$). Both males and females brought primarily medium-sized prey to the nest (55% and 59% of prey items, respectively). In addition, males and females did not differ in the ratio of adult to larval insects brought to the nest ($F_{1,12}$ = 2.25, $P > 0.05$).

Effect of brood size.—Brood size had no effect on parental feeding rates ($F_{2,19}$ = 0.18, $P > 0.05$). Chats also exhibited no differences in the number of prey delivered per visit to broods of different sizes ($F_{2,20}$ = 1.78, $P > 0.05$), with adults delivering an average of

1.42 ± 0.05 items/visit (n = 113) to broods of two, 1.47 ± 0.03 items/visit (n = 406) to broods of three, and 1.68 ± 0.04 items/visit (n = 192) to broods of four. Similarly, we found no difference in the size of prey brought to different sized broods ($F_{2,19}$ = 0.44, P > 0.05). There was, however, a difference in the ratio of adult to larval prey brought to different-sized broods ($F_{2,19}$ = 4.62, P = 0.023).

Effect of nestling age.—The feeding rates of adult chats did not vary with nestling age ($F_{5,26}$ = 1.72, P > 0.05). Similarly, the number of prey items delivered per visit ($F_{5,26}$ = 1.44, P > 0.05) and the size of prey delivered ($F_{5,26}$ = 0.73, P > 0.05) did not differ with nestling age. For all ages, the most frequent prey size was medium. For size of prey delivered, there was a significant interaction between brood size and nestling age ($F_{9,18}$ = 2.31, P = 0.046). However, examination of our data revealed that this interaction resulted from one unusual observation period at one nest. During one 6 h observation period at this nest (with a 7-day old brood of 4), adults (male and female combined) made only five visits and delivered primarily small prey items. The reason for this atypical behavior was unclear.

The ratio of adult to larval insects delivered to nestlings varied with nestling age ($F_{5,24}$ = 3.22, P = 0.023), and there was a significant interaction between brood size and nestling age ($F_{9,24}$ = 2.55, P = 0.032). Significance in these cases (as well as the significant difference in adult-to-larvae ratios among brood sizes noted previously) was due to the atypical provisioning behavior of two chats. Each of these two chats (a female with an 8-day old brood of 4 and a male with a 3-day old brood of 4) delivered an atypical number of adult insects to their nestlings during a single observation period. The female delivered 19 adult insects (and just one larva) during one observation, while, also during one observation, the male delivered 13 adult insects (and just one larva). The reason for the unusually high adult-to-larvae ratios during these two observation periods (ratios for other observations never exceeded 3.4) was unknown.

DISCUSSION

Reasons for the apparent absence of parental care by one parent at five nests are unclear. At two of the nests where the adult female was not observed feeding young, the female was not observed during the period of videotaping and, therefore, may have deserted or been killed by a predator. However, the non-feeding adult was known to be present in three of these territories. It is possible that these non-feeding chats were simply more wary than their mates and only refrained from feeding young when camcorders were present. It is also possible that, for unknown reasons, a single adult was responsible for most or all provisioning of the young at these nests. Nesting success (young fledged/nest) was lower at chat nests where only one adult appeared to be provisioning nestlings. Bart and Tornes (1989) summarized the results of 15 studies in which adult males were temporarily removed during the nestling period and concluded that, for many species, male removal results in decreased survival of young. Our results, and those of other investigators, indicate that biparental care may improve reproductive success and, as a result, may be an important factor in the maintenance of socially monogamous mating systems (e.g., Leffelaar and Robertson 1986, Lyon et al. 1987).

Males vs females.—Male and female Yellow-breasted Chats fed nestlings at similar rates and brought similar numbers of prey items of similar size with each nest visit. Similar behavior has been reported in several other species (Best 1977, Knapton 1984, Breitwisch et al. 1986, Leffelaar and Robertson 1986, Lyon et al. 1987, Smith et al. 1988, Dittami et al. 1991, Haggerty 1992). In other passerines, females (Nolan 1978, Pinkowski 1978, Howe 1979) or males (Biermann and Sealy 1982, Johnson and Best 1982) provide more food.

The reasons for these differences among socially monogamous species are not clearly understood (Breitwisch et al. 1986). At least two factors may contribute to variation in levels of male parental care and, more specifically, to the relatively high levels of parental care exhibited by male chats. First, opportunities to engage in extra-pair copulations vary among populations and species and males may seek copulations with other females according to the costs and benefits of provisioning his own offspring (Birkhead and Møller 1992). Consequently, if male parental care is important, a male should spend more effort on parental

duties than on the acquisition of additional copulations (Birkhead and Møller 1992).

Second, the population sex ratio may dramatically influence levels of male parental care (Breitwisch et al. 1986). For example, if the sex ratio is male-biased, males probably have little opportunity to change mates or acquire additional females. As a result, females may demand a level of parental care greater than males would give if they could obtain additional mates (Breitwisch et al. 1986). In contrast, if the breeding adult sex ratio is unity or female-biased, males might be able to decrease their level of parental care with no decrease in fitness. This could occur because females might compensate for a reduced level of male parental care or the rate of weight gain by nestlings might decrease very little, and young would fledge at only slightly lighter weights. In both cases, males may not experience a reduction in fitness (Breitwisch et al. 1986).

Effect of brood size.—Feeding rates of adult chats did not vary with brood size. As a result, each nestling in broods of two was fed more frequently than those in broods of three or four. Similar results have been reported in Eastern Bluebirds (Pinkowski 1978), Nashville Warblers (*Vermivora ruficapilla*; Knapton 1984), Western Bluebirds (*Sialia mexicana*; With and Balda 1990), and Northern Mockingbirds (Breitwisch et al. 1986). Although adults could potentially compensate by bringing more prey per visit or larger prey to larger broods (Biermann and Sealy 1982, Haggerty 1992), our results indicate that adult chats did not do so. Similar observations have been reported in Gray Catbirds (Johnson and Best 1982), Nashville Warblers (Knapton 1984), and Northern Mockingbirds (Breitwisch et al. 1986). Thus, in chats as in several other species, individual nestlings in larger broods apparently receive less food than those in smaller broods. Such results suggest either that nestlings in larger broods grow more slowly and, perhaps, weigh less at fledging or, if not, that food requirements per nestling decrease as brood size increases. Although limited, our data suggest that nestling mass does not vary significantly with brood size. [We found no significant difference ($z = 0.3$, $P > 0.05$) in mass between nestlings in broods of three ($\bar{x} = 15.38 \pm 0.70$ g; $n = 5$ broods) and broods of four ($\bar{x} = 15.18 \pm 0.76$ g; $n = 3$ broods) at five days post-hatching.] Thus, it appears that food requirements per nestling may decrease with increasing brood size. This has been suggested for other species (Best 1977, Walsh 1978, Pinkowski 1978, Johnson and Best 1982) and may be the result of differences in thermoregulatory costs. That is, the ratio of exposed surface area to biomass decreases with increasing brood size, resulting in lower thermoregulatory costs per nestling (Royama 1966, Mertens 1969, Seel 1969).

Effect of nestling age.—The feeding rates of adult chats did not vary with nestling age. In addition, the number of prey items delivered per visit and the type of prey (adult vs larval insects) delivered to nestling chats were not affected by nestling age. In contrast, several investigators have reported that parental feeding rates (Pinkowski 1978, Walsh 1978, Biermann and Sealy 1982, Breitwisch et al. 1986) and the volume of food delivered per visit (Johnson and Best 1982, Breitwisch et al. 1986, Haggerty 1992) increased with increasing nestling age. Previous workers also have noted that recently hatched nestlings may receive different prey than older nestlings, with younger nestlings receiving more larvae than older nestlings (Pinkowski 1978, Grundel and Dahlsten 1991). For example, Haggerty (1992) reported that 0–2 day old nestling Bachman's Sparrows received more lepidopteran larvae than did older nestlings.

In summary, our decision to delay observations until nestling chats were at least 3 days old (and 4 days old at some nests) may be the reason for the absence of changes in the provisioning behavior of adult chats with increasing nestling age. Several investigators have reported that young nestlings (1–3 days old) are visited less frequently and are provided with smaller loads than older nestlings (Bedard and Meunier 1983, Leffelaar and Robertson 1986, Haggerty 1992), and observations of nestling chats during this early period might have revealed similar behavior.

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THE EFFECTS OF MESQUITE INVASION ON A SOUTHEASTERN ARIZONA GRASSLAND BIRD COMMUNITY

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ABSTRACT.—We determined which vegetal features influenced the distribution and abundance of grassland birds at the Buenos Aires National Wildlife Refuge, Arizona. The density and distribution of mesquite (*Prosopis velutina*) exerted the strongest influence on the grassland bird community. Abundances of Pyrrhuloxia (*Cardinalis sinuatus*; $r^2 = 0.363$, $P = 0.025$) and Lucy's Warbler (*Vermivora luciae*; $r^2 = 0.348$, $P = 0.04$), and total abundance of birds ($r^2 = 0.358$, $P = 0.04$) were positively correlated with increasing density of mesquite (*Prosopis velutina*), whereas abundance of Cactus Wren (*Campylorhynchus brunneicapillus*; $r^2 = 0.452$, $P = 0.02$) was negatively correlated with increasing mesquite density. Abundance of Loggerhead Shrike (*Lanius ludovicianus*; $r^2 = 0.693$, $P < 0.001$) was positively correlated with an increasing patchiness of mesquite. Shrub-dependent bird species dominated the community, accounting for 12 of the 18 species and 557 of the 815 individuals detected. Species relying on extensive areas of open grassland were largely absent from the study area, perhaps a result of the recent invasion of mesquite into this semi-desert grassland. *Received 15 Aug. 1997, accepted 19 Mar. 1998.*

Grassland birds have declined more rapidly in the past 25 years than any other avian guild (Knopf 1994), and results from the Breeding Bird Survey indicate that less than 30% of grassland species monitored show increasing trends (Sauer et al. 1995). Habitat destruction, primarily the conversion of native grassland to agricultural land, is often implicated in these changes (Sauer et al. 1995). In much of Arizona, overgrazing by livestock is likely the most immediate threat to grassland bird communities. Buenos Aires National Wildlife Refuge, which consists almost entirely of former ranchland, currently is the largest ungrazed grassland in the state and as such represents a potentially important source of habitat for grassland birds. However, the exclusion of fire, the invasion of introduced Lehmann lovegrass (*Eragrostis lehmanniana*), and the encroachment of woody shrub species such as mesquite (*Prosopis velutina*) all have contributed to the degradation of the ecosystem.

Historical records indicate that woody shrubs were largely absent from these grasslands. Brown and Archer (1989) speculated that the introduction of livestock coupled with the exclusion of fire facilitated the lateral spread of mesquite out of riparian areas. Efforts to enhance grass production for cattle also led to the introduction of Lehmann lovegrass in the 1930s, which outcompetes native grasses and forms large, nearly monotypic stands on upland areas at the refuge.

A number of researchers have evaluated the effects of the invasion of Lehmann lovegrass into semi-desert grasslands (e.g., Bock and Bock 1988, 1992), but virtually none has focused on the effects of mesquite invasion. Germano and coworkers (1983) observed more jackrabbits (*Lepus* spp.) and Gambel's quail (*Lophortyx gambelii*) in areas with mesquite than in rangeland that had been cleared of mesquite, but beyond this there have been few quantitative studies of the connection between mesquite and bird communities in southeastern Arizona. In this study, we evaluated the relationship between bird abundance and a number of large-scale vegetation features, including the density and distribution of mesquite. Quantifying these relationships may help in understanding the changes that occur within the bird community as a result of shifts in the physiognomy and species composition of the grassland plant community.

STUDY SITE AND METHODS

This study was conducted on the Buenos Aires National Wildlife Refuge, located in the Altar Valley of

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south central Pima County, Arizona. Elevations on the Refuge range from 912–1460 m. Lehmann lovegrass is the dominant grass species in upland areas with native grasses occurring only in small, scattered patches. Mesquite is essentially the only woody species in upland areas although acacia (*Acacia* spp.), seep willow (*Baccharis* spp.), and palo verde (*Cercidium* spp.) are found occasionally.

The climate of the area is semi-arid, with an average annual rainfall of 40.5 cm. Precipitation follows the pattern typical of the southwestern United States, with 60% falling in July and August and most of the remainder occurring during winter. Temperature extremes on the refuge range from −11° C in the winter to 41° C in the summer, with an average monthly mean of 17° C.

During the autumn of 1995, we randomly placed 12 25-ha plots (1000 × 250 m) in areas dominated by the Lehmann lovegrass/mesquite cover type, and then bisected each with a 1 km transect. All transects were at least 200 m from the nearest road to minimize disturbance and any edge effect, and all transects were separated by at least 500 m to maintain independence.

We conducted bird surveys on the transects between 4 April and 17 August 1996 using a line-transect method in which all birds heard or seen within 100 m of the transect were recorded. Surveys began at sunrise and were completed by 10:00 MST. We did not conduct surveys in rain or during periods of high wind.

During the spring and summer of 1996 we sampled vegetation along the 12 transects to determine percent cover of grasses, herbs, and shrubs; density of mesquite trees; and average size of mesquite trees. To measure percent cover, we divided each of the 1 km transects into a series of 20 m segments of which a subset of 6 was randomly selected for sampling. We measured percent cover by species along these segments using the line-intercept method of Canfield (1941). As suggested by Canfield (1941), we measured grass and herbaceous cover basally and shrub cover at the crown-spread intercept.

We sampled mesquite in 10 10-m radius plots on each transect. The plots were established every 100 m at a random distance (≤60 m) perpendicular to each transect. Within each plot, we measured the height and width of all trees that were taller than the surrounding grasses. We found that tree height and width were directly related (r = 0.949, P < .001), so we arbitrarily chose height as a representative measure of size.

Using simple linear regression, we evaluated the relationship between bird abundance and the following vegetation features: overall grass cover, percent cover of native grasses, percent cover of Lehmann lovegrass, average size of mesquite trees, and density of mesquite trees. Only bird species for which we had at least 20 observations were considered. In addition, we assessed the effect of environmental patchiness by comparing bird abundance with the coefficient of variation of mesquite density, again using simple linear regression. All statistical analyses were performed using SigmaStat version 2.0 (Jandel Scientific), PC version.

RESULTS AND DISCUSSION

The density and distribution of mesquite trees were the only measured features that influenced bird abundance on the study area. Mesquite densities ranged from approximately 111–255 trees/ha, but despite the relatively high densities, mesquite trees tended to be patchily distributed and thus all of the plots retained at least some open grassland.

Total bird abundance was positively correlated with an increasing density of mesquite (Fig. 1a; r^2 = 0.358, P = 0.04, n = 12), probably the result of a number of species showing a positive, yet non-significant, relationship with mesquite density. In a study conducted at the nearby Santa Rita Experimental Range, Maurer (1985) also found total songbird density to be greater in mesquite savannah than in open grassland, although density in the two vegetation types varied throughout the season depending on the nesting phenology of the dominant species in each type.

The abundances of Pyrrhuloxia (*Cardinalis sinuatus;* Fig. 1b, r^2 = 0.363, P = 0.025, n = 12) and Lucy's Warbler (*Vermivora luciae;* Fig. 1c, r^2 = 0.348, P = 0.04, n =12) were positively correlated with increasing density of mesquite. Maurer (1985) also found both of these species to be more abundant in areas with high densities of mesquite, which fits well with previous descriptions of breeding habitat for these species. Pyrrhuloxia is considered to be a species of shrubby edges, often building their nests in mesquite trees (Bent 1968). Lucy's Warblers are foliage gleaners as well as being one of two North American cavity-nesting warblers and thus are likely to be dependent on mesquite for both foraging and nesting within the study area (Ehrlich et al. 1988). Based on these habitat requirements, it is unlikely that either of these species would have been widespread in these grasslands prior to the invasion of mesquite.

Not all species responded positively to increasing mesquite density. Cactus Wrens (*Campylorhynchus brunneicapillus*; Fig. 1d, r^2 = 0.452, P = 0.02, n = 12) were less abundant in areas of dense mesquite, although the exact nature of this relationship is not clear. McGee (1985) and Farley and Stuart (1994) reported that Cactus Wrens prefer nesting in

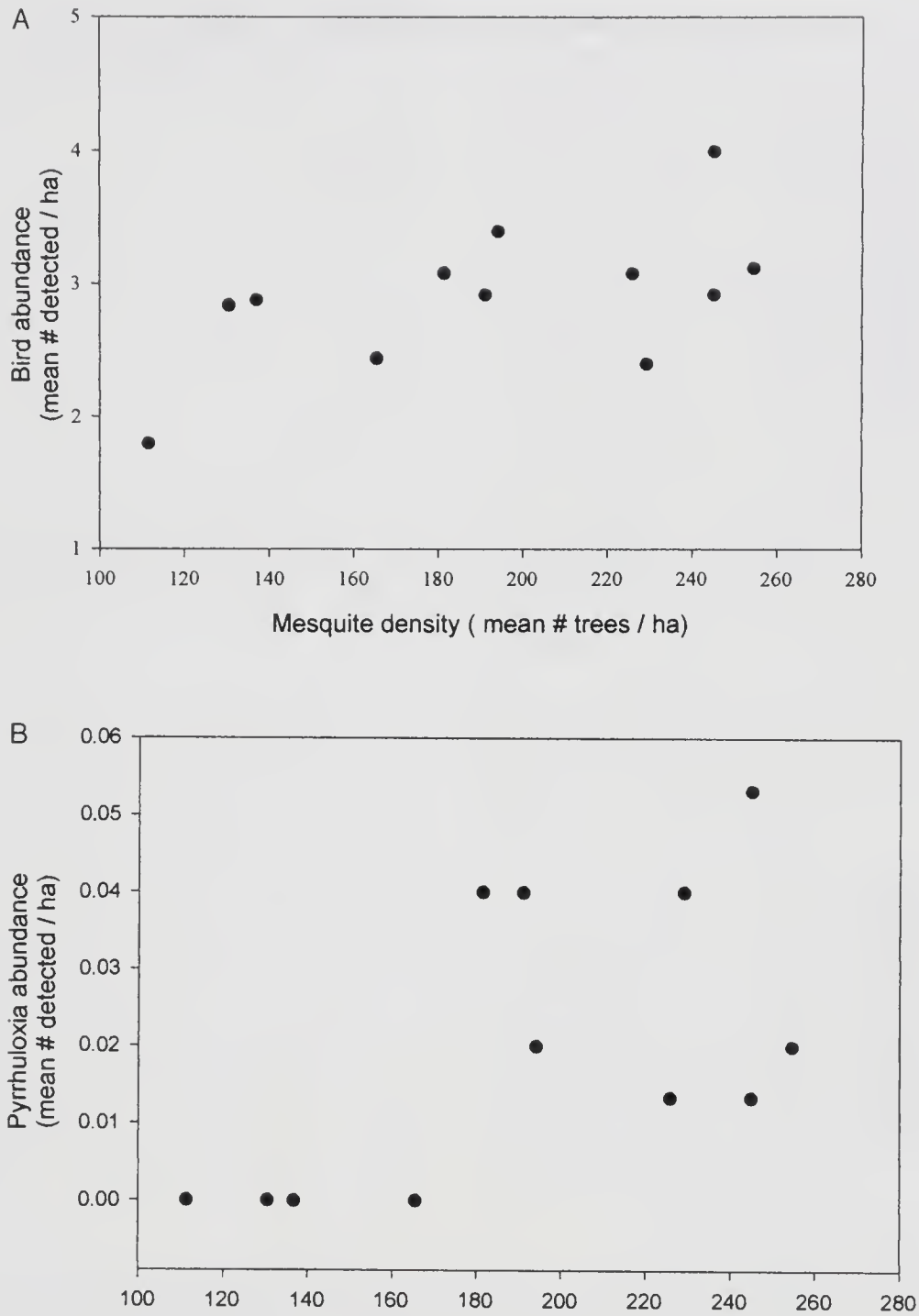

FIG. 1. Relationship between mesquite density and bird abundance on 12 study plots at Buenos Aires National Wildlife Refuge, Arizona. A. All species combined, B. Pyrrhuloxia, C. Lucy's Warbler, D. Cactus Wren.

cholla cacti (*Opuntia* sp.), which we observed to be absent from areas with a high density of mesquite. Thus, Cactus Wrens may be responding to the absence of their preferred nesting substrate rather than to changes in mesquite density. Nonetheless, a similar relationship was reported by Maurer (1985) in which Cactus Wrens were found occupying grassland sites at much greater densities than in mesquite savannah sites.

Although they did not respond directly to mesquite density, the abundance of Loggerhead Shrikes (*Lanius ludovicianus*) was positively correlated with an increasingly patchy distribution of mesquite ($r^2 = 0.693$, $P < 0.001$, $n = 12$). Again, this result is not surprising given the ecological requirements of the species. Loggerhead shrikes rely upon elevated perches in open areas from which to hunt their prey, and thus would benefit from

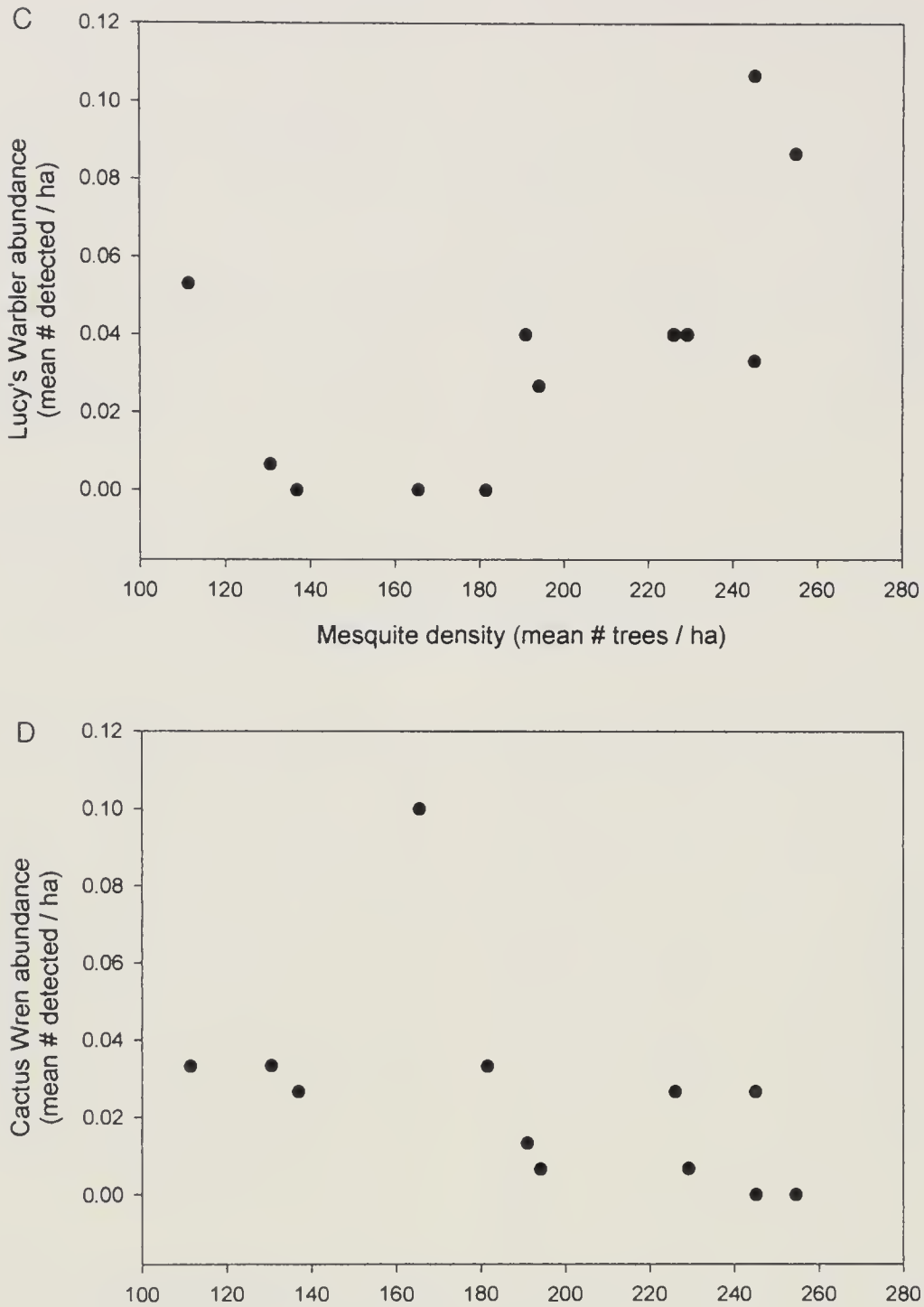

FIG. 1. Continued.

a mix of open grassland and scattered mesquite (Porter et al. 1975, Johnsgard 1986).

In addition to affecting the abundance of individual species, the spread of mesquite appears to have altered the overall bird species composition of grassland areas at the refuge. Of the 18 species for which we had at least 10 observations and which were known to breed on the refuge, 12 are species dependent on the presence of a shrub component (Table 1). This is reflected in the greater bird species richness found on plots with higher mesquite densities (r^2 = 0.491, P = 0.01, n =12). In addition to accounting for most of the species richness in this community, shrub-dependent species make up roughly 70% of the individuals present on the study area (Table 1). Maurer (1985) reported similar patterns, with shrub-dependent species accounting for roughly 60% of overall songbird density. This pattern of dominance by shrub-dependent species has likely come about only recently. Based on the records of early settlers these grasslands historically would not have provid-

TABLE 1. Total bird detections on transects at the Buenos Aires National Wildlife Refuge, Arizona, April to August 1996.

Species	Total number detected	Shrub-dependent?[a]
Black-throated Sparrow (*Amphispiza bilineata*)	251	Y
Eastern Meadowlark (*Sturnella magna*)	101	N
Lucy's Warbler (*Vermivora luciae*)	65	Y
Cassin's Sparrow (*Aimophila cassinii*)	57	N
Cactus Wren (*Campylorhynchus brunneicapillus*)	46	N
Ash-throated Flycatcher (*Myiarchus cinerascens*)	46	Y
Northern Mockingbird (*Mimus polyglottos*)	45	Y
Pyrrhuloxia (*Cardinalis sinuatus*)	36	Y
Loggerhead Shrike (*Lanius ludovicianus*)	33	Y
Mourning Dove (*Zenaida macroura*)	23	N
Blue Grosbeak (*Guiraca caerulea*)	21	Y
Botteri's Sparrow (*Aimophila botterii*)	17	N
Western Kingbird (*Tyrannus verticalis*)	14	Y
Brown-headed Cowbird (*Molothrus ater*)	14	Y
Horned Lark (*Eremophila alpestris*)	14	N
Bullock's Oriole (*Icterus bullocki*)	11	Y
Canyon Towhee (*Pipilio fuscus*)	11	Y
Verdin (*Auriparus flaviceps*)	10	Y

[a] Based on Bent 1968, Whitmore 1981, Ehrlich et al. 1988, Webb and Bock 1990, Farley and Stuart 1994.

ed suitable habitat for species requiring extensive shrub coverage (W. Kuvlesky, pers. comm.).

Although mesquite invasion has probably enhanced bird species richness in these semidesert grasslands, it may have diminished their suitability for grassland obligate species. For example, Grasshopper Sparrows (*Ammodramus savannarum*) were absent from the study area during the breeding season, although they did breed in nearby areas and were present on the study area during the winter. Grasshopper Sparrows rely on open grasslands and are thought to be sensitive to the encroachment of woody shrubs (Whitmore 1981), thus it may be reasonable to assume that the invasion of mesquite has resulted in a loss of habitat for this species.

Although most of the recent research on bird communities in the semidesert grasslands of southeastern Arizona has focused on the consequences of exotic grass invasion, our findings indicate that the spread of mesquite likely has had strong effects on the grassland avifauna as well. In fact, based on our knowledge of past conditions and on the habitat requirements of the species found within the study area, it is likely that much of the refuge now supports a very different bird community than was historically present, primarily as a result of shrub encroachment. Thus, ecosystem restoration efforts, which have until now been focused mainly on eliminating exotic grasses, should also include steps to reduce the density and extent of mesquite within traditionally open grasslands.

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Short Communications

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Conspecific Collisions Can Precipitate Mortality in Migrating Eared Grebes

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ABSTRACT.—Collisions between flying birds are a negligible problem for most species, but they may be a regular hazard for Eared Grebes (*Podiceps nigricollis*) in migration. This is a consequence of many aspects of the grebes' biology, including their massing at staging areas, early winter migrations, nocturnal movements, and poor agility in flight. *Received 13 January 1998, accepted 3 May 1998.*

Mono Lake, California, and Great Salt Lake, Utah, are the major staging areas for Eared Grebes (*Podiceps nigricollis*) in North America. Hundreds of thousands congregate there through the fall, remain until food runs out, and then fly at night to wintering grounds in southern California and Mexico (Jehl 1988). During these flights, large numbers of migrants sometimes crash and die after they lose their bearings in snow or fog (Jehl 1996). Mortality ensues from the trauma they suffer on impact with the ground or other fixed objects. In some cases the stage for mortality, if not actual death, may be set a few moments earlier, when migrants collide with each other in flight.

On the night of 13–14 January 1997, thousands of grebes migrating southward from Great Salt Lake flew into a snowstorm and crashed in southern Utah. Near the town of Delta about 3650 hit the ground after being attracted to lights of houses; of these 148 (4.1%) were found dead. Concurrently, 8 km away, 3600 more were downed and 1600 (44.4%) were found dead in a 2-ha pond at the Intermountain Power Project plant (IPP). Internal examination of over 1000 carcasses showed, as in previous downings (Jehl 1993), that death resulted from severe trauma (e.g., massive internal bleeding; broken bill, sternum, clavicles, legs; cranial hemorrhage; ruptured spleen or liver).

Weather-related downings of grebes are not infrequent in this area (Jehl 1996), but one aspect of the 1997 events was unusual: mortality was ten times greater at the IPP ponds than at Delta. This is counterintuitive, because even a hard landing on a pond is more survivable than flying into frozen ground. Migrants at IPP must have perceived the ponds correctly—as an oasis of open water in the Utah desert in winter—or they would not have been concentrated there.

Why the extreme difference? I suggest that the high mortality at IPP can be traced to traffic congestion, which resulted when thousands of migrants disoriented by the snowstorm homed in on the brilliant lights of the plant which can be seen for miles. In circling over the ponds while trying to land, and probably further confused by the blinding lights, many crashed together and fell to earth. Grebes at Delta were attracted by the lights of a town, but these were much dimmer in comparison. Because there were no lighted ponds at Delta to concentrate migrants, collisions were rare or lacking and the mortality rate was lower.

The notion that collisions could be a cause of mortality prompted me to re-examine several puzzling, but similar, instances among grebes staging at Mono Lake (Jehl 1988, unpubl. data). All involved carcasses found on beached-bird surveys late in the staging period: 11 November 1984 (378 birds), 28 October 1986 (43), 25 November 1994 (>600), 18 November 1996 (≈60) and 19 November 1997 (50–100). Mortality took place during the peak of the emigration period. Nearly all the birds died shortly (in most cases 1–4 days) before being discovered. All were in full migratory condition, having completed the changes in body compositon that are necessary for them to reacquire flight after hav-

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ing been flightless for a long period (Jehl 1997). Externally, they seemed to be in good shape; they were fat (mean body mass ranged from 417–442 g in the several samples) and carried enough fuel to migrate successfully to the wintering areas (Jehl 1994). Yet, most were bleeding from the mouth and some had broken bills or wings. Subsequent internal examinations (no data from 1996) revealed the same signs of extreme trauma seen in birds downed in migration. Death from trauma in 1994 was confirmed by veterinarians from the National Wildlife Health Center (L. Glaser, pers. comm.).

What caused this mortality? There is no possibility that these grebes died or sustained injuries while staging on the lake, that the injuries resulted from shooting or the secondary actions of scavengers (coyotes, *Canis latrans;* Common Ravens, *Corvus corax),* or that internal bleeding was the result of some hemorrhagic disease. None of these explain the broken bones and the timing of mortality coming at the peak of migration. The physiological condition of the birds showed that they were capable of flight. The shoreline location of the carcasses indicated that grebes died when flying over the lake. Yet, in no year was there any indication of bad weather (snow, fog, severe downdrafts) that might have caused the birds to become disoriented or to have forced them back to earth. I infer that the birds collided with other grebes as they rushed to leave the lake shortly after sunset. Most collisions must have occurred within moments of take-off because it would require no more than 10 minutes for a for a grebe to fly beyond the boundaries of the lake.

DISCUSSION

Collisions in flight are so rarely discerned (e.g., Abraham and Wilson 1997) that the possibility that they might result, directly or indirectly, in significant mortality may be hard to accept, especially by anyone who has marvelled at the intricate maneuvers of tightly-flocked shorebirds. Yet, many aspects of Eared Grebe biology interact to increase the risk of collision as birds leave staging areas.

1. Grebes stage in huge numbers; the fall flock at Mono Lake exceeds 1.5 million birds (Boyd and Jehl 1998).

2. Prior to leaving staging lakes grebes often congregate in tight flocks and their distribution on the lake is often highly clumped (Jehl 1988).

3. They migrate at night when visibility is poor.

4. They migrate in flocks. Their pre-emigration practice flights can evoke contagious behavior, which suggests that many groups are stimulated to take flight at about the same time.

5. The duration of the main emigration period is probably 2–3 weeks (Jehl 1988, unpubl. data), which means that an average of 75,000–100,000 birds leaves Mono Lake nightly. Because weather conditions cannot be assumed to be uniformly favorable in this peroid, there are surely many nights when the emigration is far larger.

6. Departures are concentrated with an hour or so after dark (Jehl 1997, unpubl. data).

7. Grebes are poor fliers, and departing migrants are heavily wing-loaded (Jehl 1994). It may also be relevant that most have not flown for weeks, if not months (Jehl 1988).

These factors suggest that collisions among departing grebes are likely to be regular, and even predictable hazards, to birds departing staging areas and need to be considered when evaluating the cause(s) of late-season mortality. Collisions can also affect migrants that have departed safely but which later become disoriented and swarm around lights. The problem is compounded by the poor maneuverability of flying grebes, whose lack of a tail makes it impossible for them to fly very slowly, turn quickly (Thomas 1997), or avoid obstacles detected at the last minute.

The risk of collisions raises several questions about grebe behavior and aerodynamics. For example: grebes fly in flocks, but unlike most nocturnal migrants are not known to call during flight; how, then, do they maintain flock integrity without colliding? Grebes cannot take off without first achieving forward momentum (from running on water). Do collisions cause them to lose momentum and plummet to earth? This seems probable because migrants are heavily wing-loaded, and because grebes cannot glide they cannot regain flight stability. Most of the collisions inferred above would have occurred at low elevations, perhaps ranging from a few meters (Mono Lake) to several hundred meters (Utah). From what height would an uncon-

trolled fall result in mortal trauma? Is there any height from which a falling grebe might be able resume flying if it had lost all forward momentum? Further observations and experiments will be instructive.

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Observations of Geese Foraging for Clam Shells During Spring on the Yukon-Kuskokwim Delta, Alaska

Paul L. Flint,[1,2] Ada C. Fowler,[1] Grace E. Bottitta,[1] and Jason Schamber[1]

ABSTRACT.—We studied the behavior of geese on exposed river ice during spring on the Yukon-Kuskokwim Delta. The predominant behavior while on the ice for both sexes was foraging; however, females foraged more than males. Visual inspection of the ice revealed no potential plant or animal food items. However, numerous small (<20 mm) clam shells (*Macoma balthica*) and pieces of shell were noted. It appeared that geese were foraging on empty clam shells. This potential source of calcium was available to breeding geese just prior to egg formation and geese likely stored this calcium in the form of medullary bone for use during egg formation. *Received 9 Sept. 1997, accepted 8 March 1998.*

Arctic nesting geese produce eggs from endogenous reserves (e.g., protein, lipid, and minerals) stored prior to the initiation of egg laying (Ankney and MacInnes 1978). Mineral reserves, particularly calcium, are deposited in the form of labile medullary bone (Simkiss 1967). Females build calcium depots prior to breeding and utilize this reserve when calcium demands for egg shell production exceed dietary intake (Krapu and Reinecke 1992). However, calcium is not always readily available for pre-breeding consumption and this limitation in medullary bone production may be an important factor influencing clutch size in some waterfowl species (Alisauskas and Ankney 1994).

The Yukon-Kuskokwim Delta supports large numbers of breeding Emperor Geese (*Chen canagica*), Cackling Canada Geese (*Branta canadensis minima*), Black Brant (*Branta bernicla nigricans*), and Greater White-fronted Geese (*Anser albifrons*) (Mickelson 1975). All 4 species arrive between late April and early May and begin nesting 1–3

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wks later (Mickelson 1975, Raveling 1978). Raveling and coworkers (1978) concluded that female Cackling Canada Geese stored calcium after their arrival on the breeding grounds. Prior to nesting, geese forage primarily on plant material (e.g., Budeau et al. 1991). Because the calcium content of most waterfowl plant foods is relatively low (Krapu and Reinecke 1992), breeding geese must obtain calcium from some source other than normal forage. Other potential sources of calcium for breeding geese on the Yukon-Kuskokwim Delta are unknown.

For each of the last 10 years, we have observed geese apparently foraging on snow-free river ice in spring. The use of this habitat, and certainly this behavior while on the ice, seemed unusual. Our goal in this study was to investigate and describe this seemingly anomalous behavior of geese using river ice in spring. We interpret these behaviors in relation to other studies regarding calcium intake and storage.

METHODS

We conducted systematic behavioral observations of geese using a 500 m seetion of river ice in May 1997. Pairs of geese were observed with a variable power telescope. The first pair observed to fly onto the ice within view was selected for observation. Behaviors were recorded for both the female and male every 15 see. Behavior classes used were foraging (ineluding scarching), alert, roost, walk, preen, swim, and aggression. Sex was determined by body shape as females tend to have more distended abdomens in spring (Gauthier and Tardif 1991, Johnson and Sibly 1993). Each observation eontinued until the pair departed the river iee. The proportion of time each member of a pair spent foraging while on the iee was ealculated. Each member of a pair represented a single datum, and mcans and standard errors for each sex were calculated accordingly. Pereent time foraging was compared among the sexes using a Z-test (Pollock et al. 1989).

We conducted general visual inspeetions of river ice on numerous oeeasions looking for potential food items. Intensive visual inspections of the river ice in speeifie loeations used by foraging geese were conducted on three oeeasions and variably sized samples of melt-water, sediment, and ice were collected. Ice samples were thawed and all samples were visually inspected for potential food items.

RESULTS

We collected data on 26 pairs of geese from 15–17 May 1997 (15 pairs of Cackling Canada Geese, 8 pairs of Black Brant, 2 pairs of Emperor Geese, 1 pair of White-fronted Geese). Average time spent on the river ice for a pair was 16.8 ± 2.7 min. SE (range 1–49 min.). Foraging was the most common behavior and females spent more time foraging while on the ice than males ($Z = 2.25$, $P < 0.01$; Table 1). We found no potential food items (i.e., plants or invertebrates) during visual inspection of specific foraging sites. We did observe numerous small (<20 mm length) clam (*Macoma balthica*) shells and pieces of clam shell on top of the ice. All of the shells we observed were empty and lacked any potential source of protein.

TABLE 1. Percentage of time spent in each behavior by 26 pairs of geese using exposed river ice during spring on the Yukon-Kuskokwim Delta, Alaska.

	Females		Males	
Behavior	Mean	SE	Mean	SE
Forage	73.5	3.7	54.5	4.4
Alert	12.5	3.3	28.1	3.6
Walk	9.0	1.6	10.5	1.9
Roost	3.4	1.7	3.2	1.7
Preen	1.0	0.5	2.8	0.9
Swim	0.6	0.5	0.0	0.0
Aggression	0.0	0.0	0.8	0.5

DISCUSSION

It appeared that geese likely were consuming clam shells while foraging on river ice during early spring on the Yukon-Kuskokwim Delta. Observations similar to ours have been reported for nesting Northern Pintails (*Anas acuta*) which consumed empty snail shells during egg laying (Krapu and Swanson 1975), and in the extreme case of King Eiders (*Somateria spectabilis*) consuming small bones (Uspenski 1972 *in* Krapu and Reinecke 1992). This behavior suggests that calcium availability during reproduction may be limited for some species.

Calcium content of most waterfowl plant foods is relatively low (Krapu and Reinecke 1992). Consequently, it may be difficult for females of some species to build calcium reserves prior to the initiation of egg laying. In fact, Alisauskas and Ankney (1994) concluded that insufficient mineral reserves might limit egg formation of Ruddy Ducks (*Oxyura jamaicensis*). Although based on small sample sizes, Raveling and coworkers (1978) thought

that female Cackling Canada Geese stored calcium after their arrival on the breeding grounds. Raveling (1979) thought that the observed increase in skeletal mineral content prior to nest initiation was sufficient to account for most of the calcium required for clutch formation. Foraging on clam shells may explain how female Cackling Canada Geese obtain calcium after arrival on breeding grounds.

Medullary bone serves as the storage site of minerals that may be ingested at variable rates during the day but are required at constant rates during egg shell formation (Alisauskas and Ankney 1992). This ability to store calcium may explain the short duration of the foraging bouts we observed. In a short period of time female geese likely are able to ingest large amounts of calcium which is then stored for shell production in the form of medullary bone. It is unclear why male geese would consume clam shells since males do not experience the high calcium demand associated with egg production. It may be that males (and potentially females) are consuming clam shells as a source of grit since there are no sources of grit on or near our study area. Thus, for females the ingestion of clam shells may serve a dual function as grit and enhancement of calcium reserves.

The clam shells we observed were associated with a thin layer of sediment on top of the river ice. It is unknown how this material becomes incorporated into the river ice. Typically, the river ice breaks up about the time that nest initiation commences so these clam shells are available to nesting geese just prior to the peak calcium demand. Additionally, we have observed geese foraging on ice floes moving with the tide after the river ice had broken which suggests the limited availability of alternative sources of comparable forage. We have generally noted clam shells on the river ice, and geese using river ice habitats each spring since 1987. Thus, it is likely that this habitat may provide an important and annually consistent source of calcium and/or grit for breeding geese on the Yukon-Kuskokwim Delta.

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Inter-island Dispersal of the Mariana Common Moorhen: A Recolonization by an Endangered Species

David J. Worthington[1, 2]

ABSTRACT.—Mariana Common Moorhens (*Gallinula chloropus guami*) rapidly colonized a human-made wetland on the Island of Rota in Micronesia. Although prehistoric evidence suggests that moorhens once occurred on Rota, the historic lack of wetland habitat prior to construction of an artificial wetland apparently precluded more recent occupation. This recolonization demonstrates that moorhens can rapidly exploit newly available habitat by dispersing significant distances (at least 77 km) over open ocean. *Received 25 Aug. 1997, accepted 14 March 1998.*

The Common Moorhen (*Gallinula chloropus*) is nearly cosmopolitan in distribution and is dependent on freshwater marshes with emergent vegetation (Ripley 1977, Taylor 1996). In the Pacific, it occurs on many islands with suitable wetland habitat. *Gallinula chloropus sandvicensis* is a resident of Kauai and Oahu in the Hawaiian Islands (Engilis and Pratt 1993), and *Gallinula c. orientalis* is a rare resident in Palau (Engbring 1988, Pratt et al. 1980, Taylor 1996). In the Mariana Islands, the Mariana Common Moorhen (*G. c. guami*) is endemic to Guam, Tinian, and Saipan, but was recently extirpated from Pagan. Ash deposition from a volcanic eruption, together with feral ungulates and introduced fish, eliminated the remaining habitat in 1981 (Stinson et al. 1991; Stinson 1993, 1994, 1995). Between 300 and 400 moorhens remain in the Mariana Islands (Stinson 1995). Both *G. c. guami* and *G. c. sandvicensis* are listed as federally endangered (USFWS 1984).

The Mariana Island archipelago comprises the 14-island U.S. Commonwealth of the Northern Mariana Islands and the Territory of Guam (Fig. 1). The 15 islands extend 750 km between 13° 14′ N, 144° 45′ W and 20° 3′ N, 144° 54′ W, about 1500 km east of the Philippine Islands. Though volcanic in origin, the islands where moorhens occur are largely forested limestone plateaus. The climate is tropical, with daily mean temperatures of 24-32° C and average annual rainfall of 200–260 cm.

Paleobiological evidence indicates that the Mariana Common Moorhen occurred prehistorically on the small (85 km^2) island of Rota (Steadman 1992) approximately 1500–2000 ybp (Becker and Butler 1988) but were extirpated, possibly by human-related losses of wetlands (Steadman 1992), or the natural elimination of wetland habitat over time caused by sea-level changes (Stinson et al. 1991). Hunting, introduced rats, or cats may also have contributed to the loss of moorhens from Rota (Steadman 1992, Stinson et al. 1991). There is no historic evidence of this species on Rota (Baker 1951).

Construction of an 18-hole golf resort on the north coast of Rota began in 1992. The waste water treatment plant for the resort includes two 0.6 ha primary stabilization ponds and two 0.15 ha secondary polishing ponds. The primary ponds are devoid of vegetation, but the polishing ponds contain thick plantings of sedge (*Cyperus* sp.). These ponds were filled with water and planted late in 1994. Since its creation, the site has attracted a variety of migratory birds, including several species new to the island (Wiles and Worthington 1996; Worthington, unpubl. data). On 12 April 1995, an adult Mariana Common Moorhen was observed at one of the vegetated secondary ponds. This was followed on 14 June by the sighting of an adult with two juveniles approximately ten weeks old (based on Ritter 1994). Subsequent observations confirmed the presence of two adults and three juveniles; at least two of these young fledged: Three 1 month-old chicks and two more chicks of similar age were seen at the same location on 23 November 1995 and 13 April 1996 respectively, and one older chick was observed on 26 July 1996, indicating three additional cases of successful breeding. Single moorhens were

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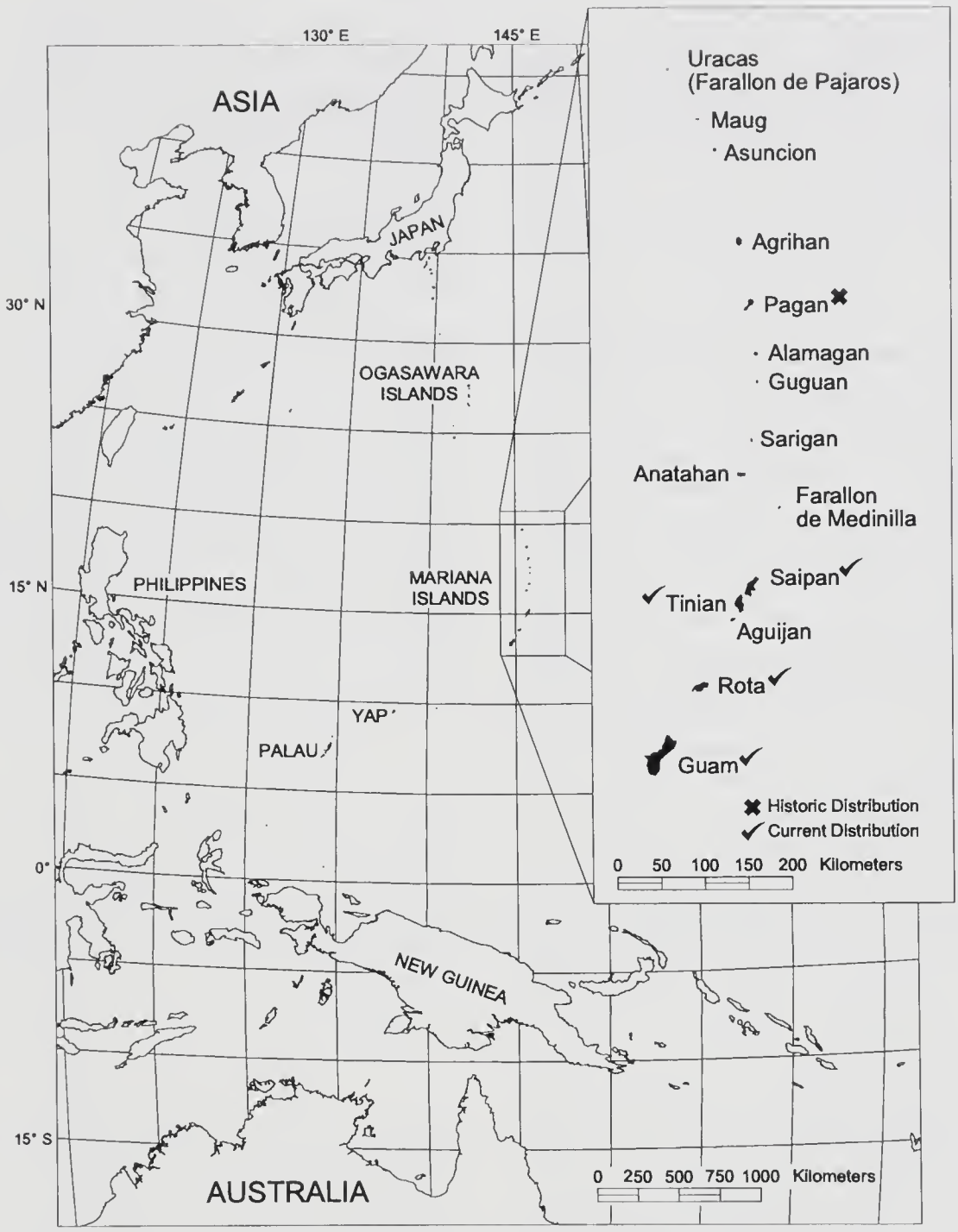

FIG. 1. Mariana Common Moorhen distribution in the Mariana Islands.

also observed in late 1995 at the golf course water hazards. One subadult was observed over 600 m from the nearest water, indicating that, as elsewhere, the birds on Rota are not exclusively restricted to wet areas. However, the lack of wetland habitat elsewhere on the island would preclude their breeding outside of the golf course property (K. Evans, pers. comm.).

Rota was probably re-colonized by moorhens migrating from one of the three Mariana islands occupied by the species. Guam lies 77 km SSW of Rota, and Tinian and Saipan are located about 120 and 127 km NNE of Rota, respectively. The birds were initially observed on Rota during the dry season (roughly January through June), the period when considerable intra-island movement of moorhens occurs on Guam (G. Wiles, pers. comm.) and on Saipan and Tinian (A. Marshall, pers. comm.). During April 1995, water was absent from Lake Hagoi on Tinian, and the number of moorhens observed during monthly counts there fell to zero from a mean of 22 birds

during the previous rainy season. No moorhens were seen elsewhere on the island during that time (S. Kruger, pers. comm.; USFWS 1996). Moorhens may fly between Tinian and the other islands seasonally, possibly regularly (Stinson 1993). Tinian lies just 5 km south of Saipan, so movement between these two islands seems likely, but remains to be documented.

The golf course treatment ponds and water hazards are presently the only permanent bodies of freshwater on Rota and are likely the reason these birds remain on Rota. Moorhens have been seen at the water hazards, which lack vegetation. Planting these ponds with emergent vegetation would likely expand the available breeding habitat on Rota. Many natural wetlands in the Mariana Islands undergo seasonal desiccation, precluding breeding by moorhens during the dry season. Human-created wetlands like the ones described here may provide year-round breeding habitat for moorhens, provided that alien species do not become established. The reed *Phragmites karka* can completely cover open water areas, eliminating moorhen habitat (Stinson et al. 1991), and tilapia (*Oreochromis mossambicus*) is an alien fish that probably competes with moorhens for food. Both of these species are invasive pests in many Mariana Island wetlands, although tilapia do not persist in ephemeral wetlands.

On Guam, moorhens have rapidly invaded human-created wetlands (Ritter and Sweet 1993), and they have been seen at newly flooded sites on Saipan (D. Stinson, pers. comm.). The species apparently is successful in exploiting scattered habitat, flying between areas at night (Roselaar 1980, Taylor 1996). Common Moorhens were not previously known on Yap, but one seen there in early July 1994 in an artificial wetland was probably a vagrant from the Philippines or Indonesia (G. Wiles, pers. comm.). The distribution of this species in the Pacific suggests that inter-island movement must have occurred historically, and these observations in Micronesia indicate that such movement continues. Nonetheless it is surprising how rapidly moorhens colonized Rota: the vegetated ponds on Rota possessed adequate cover for the birds for only a few months before moorhens were seen there. Moorhens may disperse frequently between islands, perhaps impelled by the natural desiccation of wetland habitat.

The observations described here, together with those of Engilis and Pratt (1993) and Ritter and Sweet (1993), demonstrate that human-created wetlands can provide important breeding habitat. The re-colonization of Rota shows that moorhens are capable of rapidly exploiting newly available habitat by dispersing significant distances over open ocean. Degradation and loss of natural wetlands is cited as a primary factor in the decline of moorhens in the Mariana Islands (Stinson et al. 1991, USFWS 1991). The success of moorhens in exploiting the new habitat on Rota further suggests that moorhen habitat can be augmented if the filling of wetlands that do not support moorhens is mitigated by the creation of open water wetlands when enhancement or management of existing habitat is not possible.

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The Diet of the Madagascar Red Owl (*Tyto soumagnei*) on the Masoala Peninsula, Madagascar

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ABSTRACT.—Based on pellets collected at the first known nest of this endemic species, data are presented on the diet of the Madagascar Red Owl (*Tyto soumagnei*). This owl feeds almost exclusively on small mammals, the vast majority of which are native to the island. There is evidence that this species hunts at the forest edge and uses open human-degraded habitats. There is virtually no overlap in the diet of the Madagascar Red Owl and the Barn Owl (*T. alba*). *Received 17 July 1997, accepted 10 May 1998.*

Until recently, the endemic Madagascar Red Owl (*Tyto soumagnei*) was thought to be extremely rare and restricted to primary rain forest in the eastern portion of Madagascar (Collar and Stuart 1985, Langrand 1995). Over the past five years this species has been recorded at numerous localities in eastern Madagascar, and it is becoming increasingly clear that it is at best reclusive, rather than rare, and is widespread in disturbed habitats (Halleux and Goodman 1994; Powzyk 1995; Thorstrom 1996; Goodman et al. 1996; Thorstrom et al. 1997). Although information on the distribution and natural history aspects of the Madagascar Red Owl have been significantly augmented in the past few years, certain aspects of its life history remain poorly known and some published information is contradictory to that gathered from recent field work.

With the capture and radiotagging of an adult female Madagascar Red Owl in October

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1994 and the discovery of the first known nest of this species in August 1995 near Ambanizana (see below), new information is now available on aspects of this species' ranging behavior, roosting sites, and vocalization (Thorstrom et al. 1997). Further, on the basis of a preliminary analysis of pellet and prey remains found near roosts in 1994, it is known that small mammals are the dominant prey type taken by this owl (Thorstrom et al. 1997). Herein we present further information on the food habits of the Madagascar Red Owl based on pellets collected between 1994 and 1996 near Ambanizana. These data are compared to the diet of a congeneric owl, *T. alba,* occurring sympatrically with *T. soumagnei* in the rain forests of Madagascar.

STUDY AREA AND METHODS

The study site is located near Ambanizana (15° 37′ S, 49° 58′ E), on the western side of the Masoala Peninsula, in extreme northeastern Madagascar, and is a few meters above sea level. This area of the peninsula is relatively remote and composed of a mosaic of slash and burn agricultural fields, secondary growth, and primary forests. The lowland rain forest of the area has a canopy height less than 30 m with few emergent trees and high floristic diversity. Average annual rainfall recorded at another site on the peninsula between 1992 and 1996 was 6106 mm. Monsoon rains and cyclones occur between December and April, whereas rain falls steadily between May and August (Donque 1972).

The radio-tagged adult female Madagascar Red Owl was located at 22 roost sites; 50% of the locations were at the ecotone between forest and swidden fields, 36% in rice paddies, and 14% in large areas of swidden fields. Nine diurnal roost sites were discovered during the period from October 1994 to December 1996. After the discovery of the nest, a fledgling female was radio-tagged and followed to 12 diurnal roost sites. Regurgitated pellets were collected below 3 of 9 diurnal sites for the adult and 5 of 12 for the fledgling. In 1995 and 1996, regurgitated pellets, bone and fur samples were removed from the nest by a 1 m long stick with tape wrapped at one end. The stick had a tacky tape side exposed to adhere and extract pellet material resting on the floor of the cavity.

The pellet and prey remains were identified using the comparative osteological collections at the Field Museum of Natural History. Paired bones of any taxon were separated and the largest number of elements from either the left or right side was considered the minimum number of individuals (MNI) among prey items. Body masses of identified prey species are presented in Table 1, and when possible these data are from areas in northeastern Madagascar.

RESULTS

The minimum number of individuals of the total sample was 111, representing 8 different species of land vertebrates including reptiles and mammals (Table 1). All the prey species are endemic to the island except for *Rattus rattus,* an introduced rodent. No volant animals (bats or birds) or amphibians were identified from the remains. The largest sample is from 1995, with a MNI of 78.

Endemic mammals make up the vast majority of this owl's diet both by MNI and body mass. Prey species ranged in size from the 12.8 g *Microgale cowani* to the 102.7 g *Rattus rattus.* The largest endemic mammal taken was *Eliurus webbi* with a mean body weight of 71.9 g. Over the course of the three seasons for which dietary information is available, over 99% of the MNI and biomass of prey animals were mammals. Further, endemic mammals made up the vast majority of the prey species taken, both by MNI (95%) and biomass (97%).

DISCUSSION

All of the prey species taken by the Madagascar Red Owl have been reported to occur on the Masoala Peninsula or surrounding areas (Carleton 1994, Glaw and Vences 1994, Mittermeier et al. 1994, Stephenson 1995). The majority of these species are forest-dwelling, although a few can be found at the forest edge or in disturbed habitats (e.g., *Oryzorictes hova, Microgale talazaci,* and *Microcebus rufus*). *Rattus* on Madagascar generally live commensally or in open agricultural areas, but they are also known to invade both disturbed and intact native forest. All of the native rodents in the sample, belonging to the subfamily Nesomyinae, are thought to be forest-dwelling, but several species are known to tolerate moderate levels of habitat disturbance. On the basis of this analysis, the Madagascar Red Owl predominantly hunts small mammals, and we found no evidence that frogs make up any part of its diet (contra Lavauden 1932), although in captivity this owl readily consumed frogs (Halleux and Goodman 1994).

Movements of the radio-tagged individual indicate that the maximum convex polygon home range was 210 ha (Thorstrom et al.

TABLE 1. Summary of prey remains identified from Madagascar Red Owl pellets collected at Ambanizana, Masoala Peninsula.

Species	Mean mass (g)	Source of data	1994			1995			1996			Combined		
			MNI	% total individuals	% total biomass	MNI	% total individuals	% total biomass	MNI	% total individuals	% total biomass	MNI	% total individuals	% total biomass
Reptilia														
Uroplatus sp.	~29.0	a	1	4.2	2.5	—			—			1	0.9	0.5
Mammalia														
Lipotyphla														
Oryzorictes hova	34.0	b	4	16.7	11.8	1	1.3	0.8	1	11.1	7.8	6	5.4	3.5
Microgale cowani	12.8	c	1	4.2	1.1	2	2.6	0.6	—			3	2.7	0.7
Microgale talazaci	36.0	c	5	20.8	15.7	27	34.6	23.1	3	33.3	24.7	35	31.5	21.7
Rodentia														
Eliurus minor	36.9	d	5	20.8	16.1	7	9.0	6.2	1	11.1	8.5	13	11.7	8.3
Eliurus webbi	71.9	d	7	29.2	43.8	38	48.7	64.9	3	33.3	49.4	48	43.2	59.6
Rattus rattus	102.7	e	1	4.2	8.9	1	1.3	2.4	—			2	1.8	3.5
Primata														
Microcebus rufus	41.9	f	—			2	2.6	2.0	1	11.1	9.6	3	2.7	2.2
Total for Mammalia			23	95.9	97.4	78	100	100	9	100	100	110	99.1	99.5
Total for endemic Mammalia			22	91.7	88.5	77	98.7	97.6	9	100	100	109	97.3	96.0
Total individuals			24			78			9			111		

[a] Goodman et al. (1991).
[b] Goodman et al. (1996).
[c] Goodman and Jenkins (1998).
[d] Goodman and Carleton (1998).
[e] Goodman et al. (1993).
[f] Atsalis et al. (1996).

TABLE 2. Comparison of the food habits of the Barn Owl at Andasibe and Manombo (Goodman et al. 1993) and the Madagascar Red Owl on the Masoala Peninsula.

	Barn Owl		Red Owl
	Andasibe (MNI = 176)	Manomba (MNI = 90)	Masoala Peninsula (MNI = 111)
Amphibia			
MNI	38	8	—
% total individuals	21.7	8.9	
% total biomass	4.6	0.7	
Reptilia			
MNI	2	—	1
% total individuals	1.1		0.9
% total biomass	0.1		0.5
Aves			
MNI	15	1	—
% total individuals	8.5	1.1	
% total biomass	7.4	0.8	
Native Mammalia[a]			
MNI	19	—	108
% total individuals	10.8		97.2
% total biomass	4.8		96.0
Introduced Mammalia			
MNI	102	81	2
% total individuals	57.9	90.0	1.8
% total biomass	83.1	98.4	3.5

[a] Includes *Suncus madagascariensis*.

1997). A large portion of its roost sites and home range encompass slightly to heavily disturbed habitat. The bird was not recorded in nearby closed canopy forest. The Barn Owl is a relatively common species across eastern Madagascar and is often found in open and cultivated areas. Given the roosting sites and areas that the Madagascar Red Owl apparently hunts, it is almost certain that there is some overlap in the habitat used by these two owls. The Barn Owl's diet has been studied on Madagascar at other sites. Barn Owl pellets were collected at Andasibe in an area of disturbed forest, within 400 m of a relatively intact and extensive forest block and near Manombo (Farafangana) in a disturbed and open area, about 1 km from a relatively intact natural forest (Goodman et al. 1993). In Table 2 we compare the food habits of *T. alba* from these two sites with information on *T. soumagnei* from the Masoala Peninsula. In general the vast majority of prey taken by *T. alba*, whether measured by individuals or biomass, is small mammals and almost exclusively introduced species. This is in contrast to *T. soumagnei* which feeds mostly on native small mammals.

In general, *T. alba* is a species of open habitat, avoiding closed forest throughout much of its African and Malagasy range (Fry et al. 1988, Langrand 1995). Goodman and Langrand (1993) proposed that *T. alba* was able to colonize new areas of Madagascar in the wake of the opening of forested areas and the subsequent spread of introduced small mammals. If this is indeed the case, it is conceivable that in disturbed areas, particularly at the ecotone between forest and open areas, there could be overlap in prey species between *T. alba* and other species of owls. On the basis of our dietary analysis for *T. soumagnei* and published literature on *T. alba* from rain forest sites on Madagascar, the prey species taken by these two owls is different and there is no evidence of competition for food resources between them.

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Getting Stuck: A Cost of Communal Cavity Roosting

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ABSTRACT.—Multiple Acorn Woodpeckers *(Melanerpes formicivorus)* perished as a result of two group members getting stuck while attempting to exit a communal roost cavity simultaneously. Both birds died, as did other individual(s) trapped behind them. Although communal roosting may have many benefits, such mortality constitutes a risk of communal roosting that may help explain why Acorn Woodpeckers choose not to roost as communally as they could. *Received 28 July 1997, accepted 17 April 1998.*

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Here I report an observation suggesting a potentially important cost of communal cavity roosting that may help explain its relative rarity. That communal roosting is typically advantageous is, of course, well documented. Individuals utilizing communal roosts compete for preferential access to the more protected interior roost sites (Swingland 1977, Weatherhead and Hoysak 1984), suggesting benefits of roosting both communally and in sheltered areas (Weatherhead 1983). Benefits of a sheltered roost site include not only greater protection from predators, but also lessened ex-

posure to wind and precipitation (Weatherhead 1983). Cavities, being particularly well-sheltered (Kendeigh 1961), are utilized as roost sites by various avian taxa (Ligon 1993). Although communal roosting within cavities is relatively rare in birds, individuals that do so appear to enjoy substantial thermal benefits. Eastern Bluebirds *(Sialia sialis),* for example, roost communally during inclement weather (Frazier and Nolan 1959, Zeleny 1977). The best studied communal cavity roosting birds are found among cooperative breeders. In Acorn Woodpeckers *(Melanerpes formicivorus),* up to 14 group members have been observed roosting together in the same cavity (W. D. Koenig, pers. comm.). Experiments with Acorn Woodpeckers (du Plessis et al. 1994) and Green Woodhoopoes *(Phoeniculus purpureus*; Williams et al. 1991, du Plessis and Williams 1994) demonstrated significant energetic/thermal benefits of this behavior.

The relative rarity of communal cavity roosting suggests, however, the possibility of substantial costs as well. First, cavities are often found in dead or rotten limbs, which may be susceptible to both attack by predators (Ligon and Ligon 1978) or natural breakage. Moreover, communal roosts provide a means of transmission for various parasites and pathogens (Weatherhead 1983). Crowding may even result in suffocation. Pygmy Nuthatches *(Sitta pygmaea)* have been observed roosting in aggregations of over 100 individuals within single, albeit large, cavities and dead birds have been found at the bottoms of such cavities (Knorr 1957). In a communal roost of Eastern Bluebirds, 2 of 16 birds roosting in a small cavity during a snowstorm died before morning (Zeleny 1977).

Cavity roosting birds, especially communal cavity roosters, also face the possibility of becoming trapped within cavities. I once found the contorted remains of a female Acorn Woodpecker that had become stuck in the entrance of a hole. From her position I surmised that she had tried to turn around and exit the hole before she was all the way in. Had another bird been inside the cavity when this occurred, it may well have perished inside, paying a high price for communal roosting.

Such multiple mortality was observed in 1992. Arriving at a seldom-visited Acorn Woodpecker territory off the Hastings study area, I noticed that the entire group had disappeared and been replaced by new birds. Upon investigation I found the remains of two adult male woodpeckers stuck in a single cavity entrance. They had apparently attempted to depart the hole at the same time and become stuck at their shoulders. Neither bird appeared to have been caught by their leg bands (nor has this been observed on our study area). Inspection of these bands revealed both to have been breeders at the group. After removing their dehydrated remains, I found the remains of at least one other bird (the breeding female) trapped in the cavity behind them. This cavity, the walls of which were at least 5 cm thick, was located in a live limb of a valley oak *(Quercus lobata).* The birds within the cavity were not the only victims of this incident: the surviving members of the group had apparently been unable to defend the territory from usurpers.

Other observations also suggest that the communal roosting option in Acorn Woodpeckers is not pursued to the extent that might be expected from thermal advantages alone. Although communal roosting is the norm, entire groups seldom roost together in the same cavity (W. D Koenig and M. T. Stanback, unpubl. data). Although the size of the cavity may sometimes constrain the number of birds that can roost within it, this cannot be a general explanation: a cavity in which 4 birds are observed roosting on one night might be used by only 2 birds the following night. Such observations indicate that Acorn Woodpeckers are choosing not to roost as communally as they could, perhaps as a result of the potential costs discussed above.

Examination of the roosting habits of the Red-cockaded Woodpecker *(Picoides borealis)* also suggests that communal roosting may be especially costly in this species, which maintains sticky sap wells around cavity entrances. J. Walters (pers. comm) reports several instances in which individuals of this species have been trapped in sticky cavity entrances, including some (involving nests) in which additional individuals were trapped inside as well. Perhaps it is not surprising then, that Red-cockaded Woodpeckers roost solitarily, despite the fact that roost cavity availability drives cooperative breeding in this spe-

cies (Walters 1990). This insistance on solitary roosting is not only expensive in terms of cavity construction, but is also extremely costly for those group members, usually juveniles, lacking access to their own roost hole. Such supernumerary individuals are generally forced to roost in the open (J. Walters, pers. comm.) where they are exposed to ambient temperatures, precipitation, wind, and predators. This suggests that, for the Red-cockaded Woodpecker, the costs of roosting communally within a cavity outweigh not only the costs of solitary roosting, but also the general benefits of cavity roosting.

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Anting by an American Dipper (*Cinclus mexicanus*)

Sophie A. H. Osborn[1]

ABSTRACT.—Anting behavior has been recorded in over 200 birds, yet its purpose remains unresolved. Here I report an observation of anting in an aquatic passerine, the American Dipper (*Cinclus mexicanus*). The dipper was seen preening ants onto its remiges in a process known as "active" anting. Numerous hypotheses exist for why birds ant, including controlling ectoparasites, inhibiting the growth of fungi or bacteria, soothing skin irritated during the molting period, and removing toxic formic acid prior to food consumption. Because of the timing and nature of the dipper's anting episode and the fact that dippers are not known to consume ants, my observation does not appear to lend support to either the molt-irritation or the food preparation hypotheses for this species. *Received 5 Dec. 1997, accepted 26 March 1998.*

Anting behavior, in which a bird exposes its plumage and possibly skin to ants or other pungent substances (Whitaker 1957, Simmons 1966, Clayton and Vernon 1993), has been documented sporadically in the literature and its purpose remains unresolved. Although it is observed infrequently, anting has been recorded in more than 200 avian species (see Groskin 1950, Whitaker 1957, Potter 1970, Dun-

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can 1976, Hendricks 1980, Post and Browne 1982), most of which have been passerines. To date, only one record exists for anting in an aquatic species (Creutz 1952), the Eurasian Dipper (*Cinclus cinclus*). Here, I report an incident of anting in the American Dipper (*Cinclus mexicanus*), North America's only truly aquatic passerine.

I observed an adult American Dipper anting on Blodgett Creek (elevation 1370 m), near Hamilton, Montana, on 12 July 1997. Just prior to anting, the bird was engaged in two aerial chases and attacks with another dipper. At 09:50 MST, the dipper flew to the end of a downed log that was partially submerged in water across the stream from its nest. There, it pecked into a hole (7.5 × 13.2 cm), whereupon numerous ants began to emerge. The dipper then picked up an ant and, holding its right wing open, applied it with a preening motion to the ventral portion of its wing. The entire process was then repeated, with the dipper picking up a total of approximately 15 ants. The bird concentrated its efforts primarily on the axillary and secondary regions of its right wing. It appeared to insert each ant near the base of the remiges and then to preen down toward the tips. Several ants were applied to the base of the secondaries or secondary coverts and into the axillaries without a downward preening motion. I may have overlooked anting of the bird's primaries because it was several seconds before I recognized the dipper's unusual alternation of pecking at ants and preening as anting behavior. Only one ant appeared to be used for each preening bout and each ant appeared to be held among the feathers for only a few seconds. I was not able to determine whether the dipper consumed or discarded the ants after using them. The anting bout was conducted in full sunlight and lasted 1–2 minutes. The bird did not vocalize while anting.

Ants that were later collected from inside the hole in the log were identified as *Formica neorufibarbis* (Emery). I suspect that the dipper was using this species for its anting bout because it initially pecked into the hole numerous times and then began picking up the ants as soon as they emerged. However, two other species of ants were collected from the immediate vicinity of the hole, *Camponotus vicinus* (Mayr) and *Camponotus laevigatus* (F. Smith). Both genera spray formic acid and are known to be used by anting birds (Groskin 1950). From my observation position, I could not be certain whether the dipper was selecting *Formica neorufibarbis* exclusively, or whether it also selected one or more of the *Camponotus* spp. that may have been attracted to the swarming *Formica* ants. All ants were collected approximately one month after the observation, because high water prevented my being able to access the log any earlier.

The anting I observed conforms to descriptions of "active" anting wherein a bird actively preens ants into its feathers, as opposed to "passive" anting in which birds settle on ants and allow them to crawl into their plumage (Whitaker 1957, Potter 1970). Unlike many birds that have been described as anting "frenetically" (Clayton and Vernon 1993) or while in apparent "ecstasy" (Ivor 1956), even falling over in the process, the dipper I observed appeared to ant calmly, looking much as though it were merely preening.

Numerous hypotheses exist for why birds ant. Anting may help control ectoparasites (Groskin 1950, Simmons 1966), inhibit the growth of fungi and bacteria owing to the antibiotic nature of ant secretions (Ehrlich et al. 1986), soothe skin irritated by rapid feather replacement during the molting period (Potter 1970, Potter and Hauser 1974), or be a means of removing toxic formic acid prior to food consumption (Judson and Bennett 1992). My anting observation occurred prior to the dipper's presumed molting period and therefore does not appear to lend support to the hypothesis that anting is closely correlated with feather replacement (Potter 1970, Potter and Hauser 1974). American Dippers have been recorded molting only between July and September (Bent 1948, Sullivan 1973). Dippers molt after the dispersal of their young and undergo a brief molt-induced flightless period (Sullivan 1965, 1973). The dipper I observed was still feeding its fledglings, which had left the nest three days earlier. Dippers continue to feed fledglings up to two weeks before the young disperse (Sullivan 1973). The anting dipper still retained all its remiges and rectrices and showed no obvious signs of having begun its molt. However, without having the bird in hand, I could not confirm whether it had started replacing its body feathers. Be-

cause dippers molt symmetrically (Sullivan 1973), the dipper I observed presumably would have anted both wings if its anting bout was correlated with feather replacement. Anting birds frequently have been seen alternating wings during bouts of anting (e.g., Wenny 1998). Although the female Eurasian Dipper observed by Creutz (1952) in Germany anted the ventral and dorsal sides of both wings, it did so in early April (in 1939), well before its molt. Creutz was unable to identify the object(s) with which the Eurasian Dipper anted.

Because dippers are not known to consume ants (Kingery 1996), it is also unlikely that the American Dipper I observed was anting as a means of food preparation. To my knowledge, no information exists on ectoparasites, fungal pathogens, or bacterial infections of dippers. However, dipper nestlings and nests are known to be parasitized by ectoparasites such as the northern fowl mite (*Ornithonyssus sylviarum*; Halstead 1988). A nestling dipper of fledging age I found dead in the nest (4 July 1997) in my study area was heavily infested with unidentified ectoparasites. Cause of death was unknown, yet the presence of ectoparasites suggested that adult dippers could become infested by nest and nestling parasites during brooding and/or feeding of the young. More observations of anting in the dipper are needed to adequately determine whether this aquatic species gains the same possible benefits from anting as do non-aquatic passerines.

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Single-egg Removal from an Artificial Nest by the Gray Catbird

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ABSTRACT.—Brood parasitic birds often remove an egg from host nests. At least one previous author interpreted single-egg removal from a nest as a sign of Brown-headed Cowbird (*Molothrus ater*) activity. Partial clutch reduction, however, cannot be taken as a clear indication of brood parasitic activity at natural or artificial nests because egg predators may also cause partial clutch reduction by pecking and removing some but not all eggs. Video-taping at an artificial nest baited with plastic eggs showed that the Gray Catbird (*Dumetella carolinensis*), a known egg-predator, was responsible for a single-egg removal event, even though it also pecked other eggs in the nest. Thus, partial clutch reduction in general, and single-egg removal in particular, cannot be interpreted as clear signs of either brood parasitism or egg predation. In addition, the use of plastic eggs, however convenient and realistic they may seem, is inappropriate to distinguish between the activities of brood parasites and egg predators. *Received 9 Sept. 1997, accepted 22 Jan. 1998.*

Predation at birds' nests frequently results in the loss of the complete clutch or brood while partial clutch reduction is often associated with brood parasitism (Belles-Isles and Picman 1986, Wolf 1987, Brown and Brown 1989, Burgham and Picman 1989, Soler et al. 1997; but see Sealy 1994). Several interspecific brood parasites, such as female Brown-headed Cowbirds (*Molothrus ater*), often remove one host egg per parasitized nest (Wolf 1987, Scott et al. 1992). In at least one report, single-egg removal events at natural and artificial nests were suggested to be indicators of nest discovery by brood parasites, even in the absence of subsequent appearance of parasitic eggs (Lowther 1979). However, Wolf (1987) found that in one year only 58% of Dark-eyed Junco (*Junco hyemalis*) nests actually parasitized by cowbirds had any eggs removed. In another study on Yellow Warblers (*Dendroica petechia*), only 11% of the eggs lost in parasitized nests were removed by the cowbird parasite itself (Burgham and Picman 1989). Thus, demonstration of brood parasite activity should not be based solely on partial clutch loss nor should all partial clutch losses be attributed to parasite activity. Here I report a video-taped predation attempt by the Gray Catbird (*Dumetella carolinensis*) at an artificial nest that resulted in the reduction of the clutch by a single egg. Pecking and removal of eggs from heterospecific nests by catbirds have been reported or studied extensively at few locations in North America [e.g., in Ontario by Dixon (1930), Belles-Isles and Picman (1986), and Spooner et al. (1996); in Manitoba by Sealy (1994)], and there is only one prior record of these activities of catbirds from a New York population (J. B. W. 1884).

As part of a study to determine the cues used by female Brown-headed Cowbirds to locate host nests, 15 artificial open cup nests were placed at heights between 1–2 m in low shrub habitat at the perimeter of the Cornell Experimental Ponds, Ithaca, New York, in May 1997. Two days after a nest was placed in the field, host activity was simulated by adding one egg daily to each nest for four days to reach a "clutch-size" of four (Thompson and Gottfried 1981). The eggs were not glued to the nests and all nests and eggs were acquired commercially (Birds and Accessories, Inc., Omaha, NE). The nests were made of fine dark twigs, ranged between 8–12 cm in diameter and 4–8 cm in depth, and were secured to branches using green wire twist ties. The plastic eggs were off-white with brown speckles (much like warblers' eggs), 16–20 mm in length and about 2 mm thick. I filled the eggs with dark colored water to increase their weight. The content of each nest was monitored daily, usually before noon, for 10 days; any eggs that disappeared or were found on the ground near the nests were replaced. Both nests and eggs were removed from the field at the end of the observation period.

During this study no cowbird eggs were found in any of the 15 nests, but 13 (87%)

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nests suffered partial or complete loss of content, often repeatedly. Out of 89 daily checks of nests which had contained at least two eggs the day before, 12 (13%) suffered full clutch losses while 29 (33%) suffered partial clutch losses. In 15 (52%) of 29 partial clutch losses a single egg was found missing. Perhaps because the artificial eggs were made of plastic, I could see no clear gnaw or peck marks on eggs that remained in nests or on the ground in the vicinity. The study area contained several bird and mammal species [e.g., House Wren (*Troglodytes aedon*), Red-winged Blackbird (*Agelaius phoeniceus*), Black-Capped Chickadee (*Parus atricapillus*), Brown-headed Cowbird, Common Grackle (*Quiscalus quiscula*), American Crow (*Corvus brachyrhynchos*), eastern chipmunk (*Tamias striatus*), and feral cats] that are known to prey on nests or peck and remove heterospecific eggs (Pessino 1968, Picman and Belles-Isles 1988, Picman and Schriml 1994, Sealy 1994). There were also several storms during the observation period, and I suspected that some eggs had fallen from nests simply because of strong winds. Therefore, to determine the cause of a partial clutch loss, on 15 May 1997 I set up a video camera, without a blind, 4 m from an artificial nest from which one of four eggs had been removed the previous day. Recording began at 10:00 EST and the camera's battery was replaced every 1.5–2 hrs during the day, at which times the contents of the nest were also checked. A single egg disappeared from the nest between 16:40 and 18:10. The recording showed that at 17:14 a Gray Catbird landed on a neighboring branch, erected its feathers, and approached the artificial nest. Within 20 seconds it grasped one of the eggs in its beak, lifting it from the nest, apparently trying to swallow it. It failed to do so and the egg fell to the ground (where it was later recovered). At 17:15 a second catbird arrived, hopped on the nest, and pecked into it six times, while the first bird moved away from the nest but remained within the camera's field of view. After 15 seconds the first bird approached the nest again, displaced the second individual, and delivered 19 visibly powerful pecks at the eggs. It lifted one of the eggs up to the perimeter of the nest three times before finally flying off at 17:17 without having removed any more eggs. No other animal approached the vicinity of the nest for the rest of the duration of the tape and no other nests were video-taped in 1997.

Until recently, the Gray Catbird itself was not recognized as a frequent and wide-spread nest-predator because there were few published observations on its egg-pecking habit (Dixon 1930, Pearson 1936, Bent 1948). However, Sealy (1994) observed, and Belles-Isles and Picman (1986) and Spooner and coworkers (1996) showed experimentally that Gray Catbirds often attack natural and artificial nests and peck, destroy, and consume eggs. In these studies catbirds always removed and damaged more than one egg when available. Two previous records of single-egg removal by catbirds were cited by Bent (1948), but when checking the source of one of those records (J. B. W. 1884), I found that it mentions the catbird breaking the heterospecific egg, not removing it.

Partial clutch reduction at birds' nests may be caused by inter- and intra-specific predators, competitors for nest sites and habitat, brood parasites, nest-owners themselves, and non-biological factors, such as strong winds and heavy rains (Sealy 1994). Single-egg removal events are known to result from the actions of several of these agents (Bent 1948, Pessino 1968, Wolf 1987, Brown and Brown 1989, Sealy 1994, Soler et al. 1997) and thus, in the absence of additional information, partial clutch reduction (including single–egg removal) cannot be attributed to any one factor unambiguously. In particular, the list of previously unknown passerine egg predators has increased in recent decades, partially as a result of the use of more direct approaches in studies of nesting success (e.g., personal monitoring: Picman and Belles-Isles 1988, Sealy 1994; photo- or videography: Picman and Schriml 1994), suggesting that nests may be attacked at varying frequencies by species that we may not have suspected before. In addition, I found that the relative frequencies of single-egg versus multiple-egg removal by brood parasites and nest predators are difficult to quantify from published observations because several researchers that used artificial nests placed only one egg per nest (Belles-Isles and Picman 1986, Picman and Schriml 1994) or reported only on rates of "nest-disturbance and failure" without further details

on egg removal patterns (Gottfried and Thompson 1978, Yahner and DeLong 1992). Therefore, there is little support for the suggestion that single-egg losses can be interpreted as evidence for actions of the brood parasitic Brown-headed Cowbird (Lowther 1979).

It is possible that the catbirds in my observation did not remove or destroy more than one egg because the eggs were artificial. Based on the recorded behavior of the catbirds, had there been natural eggs in the nest, more than one egg would have been eaten and/or destroyed because, unlike plastic ones, eggs of many species can be swallowed or broken through pecking by catbirds (Belles-Isles and Picman 1986, Sealy 1994). In addition, if the artificial eggs had been made of plaster (as commonly and historically used in nest predation and egg mimicry studies; e.g., Selander and Yang 1966), I probably would have noticed characteristic peck marks on the remaining eggs in the nest. Thus, the use of plastic eggs may not be appropriate to discriminate partial clutch reductions associated with brood parasitism (in which egg removal is usually not accompanied by egg pecking; Wolf 1987) from those accompanying egg predation attempts. It also remains unknown how frequently catbirds are responsible for single-egg removal events at natural nests. Nonetheless, had I not recorded with a camera the activity of catbirds, I would not have had evidence for the catbirds' attempts to peck the other eggs so the end-of-day observation would have been a single-egg removal event. The aim of this note is thus three fold: (1) to document the occurrence of egg pecking and removal by catbirds in the Ithaca, New York, population, (2) to discourage the use of commercially available and inexpensive plastic eggs in studies of egg predation and parasitism, and (3) to caution about the interpretation of egg removal events in general, and single-egg removal events in particular, as evidence for the activities of brood parasites in the absence of direct observations.

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First Record of Shiny Cowbird (*Molothrus bonariensis*) in Yucatán, Mexico

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ABSTRACT.—Since the early 1900s, the Shiny Cowbird (*Molothrus bonariensis*) has expanded its range from northern South America through the West Indies. This spread has had detrimental effects on several species, especially endemics confined to islands. Here, I report the first record for Shiny Cowbirds in Mexico. The establishment of this species in the Yucatan Peninsula seems likely, and may pose a problem for the conservation of Yucatan endemics. *Received 18 June 1997, accepted 5 March 1998.*

The Shiny Cowbird (*Molothrus bonariensis*) has rapidly expanded its range since the turn of the century, island hopping from Trinidad and Tobago north through the Lesser Antilles, and west through the Greater Antilles (Post and Wiley 1977, Post et al. 1993). The species was first recorded in Cuba in 1982 (Garrido 1984) and in Florida in 1985 (Smith and Sprunt 1987). From the Greater Antilles, the Shiny Cowbird has been expected to invade into Florida and the Yucatan Peninsula of Mexico (Post and Wiley 1977, Howell and Webb 1995).

On 27 May 1996, I observed a single male Shiny Cowbird in an area of burned mangroves adjacent to an intact mangrove forest at the eastern edge of the town of Río Celestún, Yucatan, Mexico. Identifying field marks of the bird were a slender conical bill, uniform dull blue-black plumage, squared-off tail, and a solid dark eye. Of Yucatan resident species with which the Shiny Cowbird could be potentially confused, eye color and plumage differentiated it from Bronzed Cowbird (*M. aeneus*), and the bill and tail shape separated it from Melodious Blackbird (*Dives dives*). The appearance of Shiny Cowbird in mangrove forest is not unexpected, as this seems to be the preferred lowland habitat of the species in the Antilles (Post and Wiley 1977, Post et al. 1990).

The spread of Shiny Cowbirds through the West Indies has been favored by the conversion of forested areas to early successional habitats, and by the absence of native brood parasites (Post and Wiley 1977, Cruz et al. 1995). Contact with Shiny Cowbirds has proven detrimental for some West Indian bird species, particularly the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*) and the Puerto Rican Vireo (*Vireo latimeri*; e.g., Post and Wiley 1976, Post 1981, Wiley et al. 1991, Faaborg et al. 1997). Birds that have no evolutionary experience with brood parasites may suffer high rates of parasitism and reproductive failure (Wiley 1985, Post et al. 1990, Cruz et al. 1995).

Eventual establishment of Shiny Cowbird populations in the Yucatan Peninsula seems likely, given that 25% of the region's forest has been converted to agriculture (Toledo and Ordóñez 1993). Yucatan birds may not be as vulnerable to brood parasitism as West Indian birds because of contact with the Bronzed Cowbird, which is resident throughout the Peninsula. However, experience with the Bronzed Cowbird may be limited among Yucatan birds because this species is less of a generalist parasite, specializing mostly on ic-

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terids and finches (Friedmann 1929, Oberholser 1974). Thus, the presence of two sympatric brood parasites in the Yucatan may be detrimental to more species.

During the early years of Shiny Cowbird range expansion (1920–1940), its primary hosts on Trinidad and Tobago included the House Wren (*Troglodytes aedon*) and Yellow-hooded Blackbird (*Agelaius icterocephalus*; Cruz et al. 1995). As the Shiny Cowbird has moved through the Antilles, frequent host species included vireos, *Dendroica* warblers, *Myiarchus* flycatchers, as well as *Agelaius* blackbirds (Wiley 1985, Post et al. 1990, Cruz et al. 1995).

The ability of Yucatan endemics to persist in light of potential establishment of the Shiny Cowbird is an important question. Based on host choice trends of the Shiny Cowbird, Yucatan endemics at risk include the Yucatan Flycatcher (*Myiarchus yucatanensis*), Yucatan Wren (*Campylorhynchus yucatanicus*), Orange Oriole (*Icterus auratus*), Black Catbird (*Melanoptila glabrirostris*), Cozumel Vireo (*Vireo bairdi*), and Cozumel Wren (*Troglodytes beani*; Friedmann 1929, Friedmann et al. 1977, Friedmann and Kiff 1985). Yucatan Vireo (*Vireo magister*) and White-browed Wren (*Thryothorus albinucha*) are regional endemics potentially also at risk of parasitism. Careful monitoring of Shiny Cowbirds on the Peninsula, and the effects on species already resident there, will be important.

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Call Mimicry by Eastern Towhees and Its Significance in Relation to Auditory Learning

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ABSTRACT.—We document cases of Eastern Towhees (*Pipilo erythrophthalmus*) using mimicked alarm calls from three presumptive models [Blue Jay (*Cyanocitta cristata*), Brown Thrasher (*Toxostoma rufum*), and American Robin (*Turdus migratorius*)]. In four instances, male towhees employed heterospecific calls without substitution in their own call repertoires. Three birds (New Jersey, New York) used jay-like calls mixed with "Chewink" calls in the same bouts of calling. One bird (New York) increased the frequency of its mimicked call during intense reactions to disturbance (high rate of calling). A Texas towhee employed jay-like and Chewink calls separately in different contexts. In another case, sequences of robin-like alarm calls were used by a towhee to form unusual, distinctive song-types during bouts of singing. These observations suggest that some aspects of towhee alarm call repertoires may be influenced by auditory learning, and that mimicked alarm calls also can be incorporated into song repertoires. *Received 22 Jan. 1998, accepted 21 April 1998.*

Although avian vocal mimicry has attracted interest for centuries (Witchell 1896, Armstrong 1975), most of what is known about development of species-typical vocal repertoires, including mimicry, is based on recent studies of sound imitation and its role in song development in songbirds (e.g., Marler and Mundinger 1971, Marler 1991). Mimicry of heterospecific and inanimate sounds can be a facultative response to sound experience, or a regular imitation of songs or calls that may be adaptive (e.g., Baylis 1982). Yet, the role of mimicry in the development of call repertoires rather than as elements of song remains poorly understood (Baylis 1982).

Eastern Towhees (*Pipilo erythrophthalmus*) rarely mimic other species. Previous cases of vocal mimicry in this species involved the use of mimicked songs or song phrases from two heterospecific models to form distinctive song types (Borror 1977, Richards 1979). Here, we report instances in which towhees mimicked the calls of several other species and used these calls in their call or song repertoires. The use of mimicked calls in call repertoires is rarely reported in songbirds. Its occurrence in towhees may indicate at least limited flexibility in the development of the call repertoire in this species.

STUDY AREAS AND METHODS

The term "vocal mimicry" is used here in a purely descriptive sense, and does not carry any functional connotation. It describes a vocalization of one species that resembles the sounds of another species (Baylis 1982). In this case, we address the specific issue of "call mimicry."

Observations of presumptive call mimicries by towhees were obtained at: (1) W. L. Hutcheson Memorial Forest (HMF), near East Millstone, Somerset Co., New Jersey (1968); (2) Kalbfleisch Field Research Station (KFRS), Dix Hills, Suffolk Co., New York (1970–1972); (3) Fire Island National Seashore (FINS), near Fire Island Lighthouse, Suffolk Co., New York (1970); (4) Muttontown Nature Preserve (MNP), Muttontown, Nassau Co., New York (1972); and (5) Big Thicket National Preserve, Tyler Co., Texas (1995). With the possible exception of the Muttontown NP towhee, all birds were territorial males. Visits to the territories of two northeastern males spanned periods from late spring to mid- (HMF) or late summer (KFRS). Multiple visits to two other males' territories extended from mid-June to July (Texas male) or to August (FINS). The Muttontown NP male was observed only once (21 March 1972), and its breeding status was unknown. A Kalbfleisch FRS male (color-banded as a hatch-year bird in August 1969) was present from 1969–1976, and we noted it using robin-like calls in his primary songs from 26 April 1970 to 10 August 1972. The Texas male was unmated, and was observed from 14 June to 2 July 1995.

Mimicked vocalizations were taped in New York and Texas using a Uher 4000L recorder, a Uher microphone in a 61 cm (24-inch) parabolic reflector (HMF), and a Dan Gibson 46 cm (18-inch) electronic parabolic microphone (KFRS, FINS), or a Uher 4000 Report IC recorder and a Dan Gibson EPM Model P-200 parabolic reflector (46 cm shield; Texas). Sound

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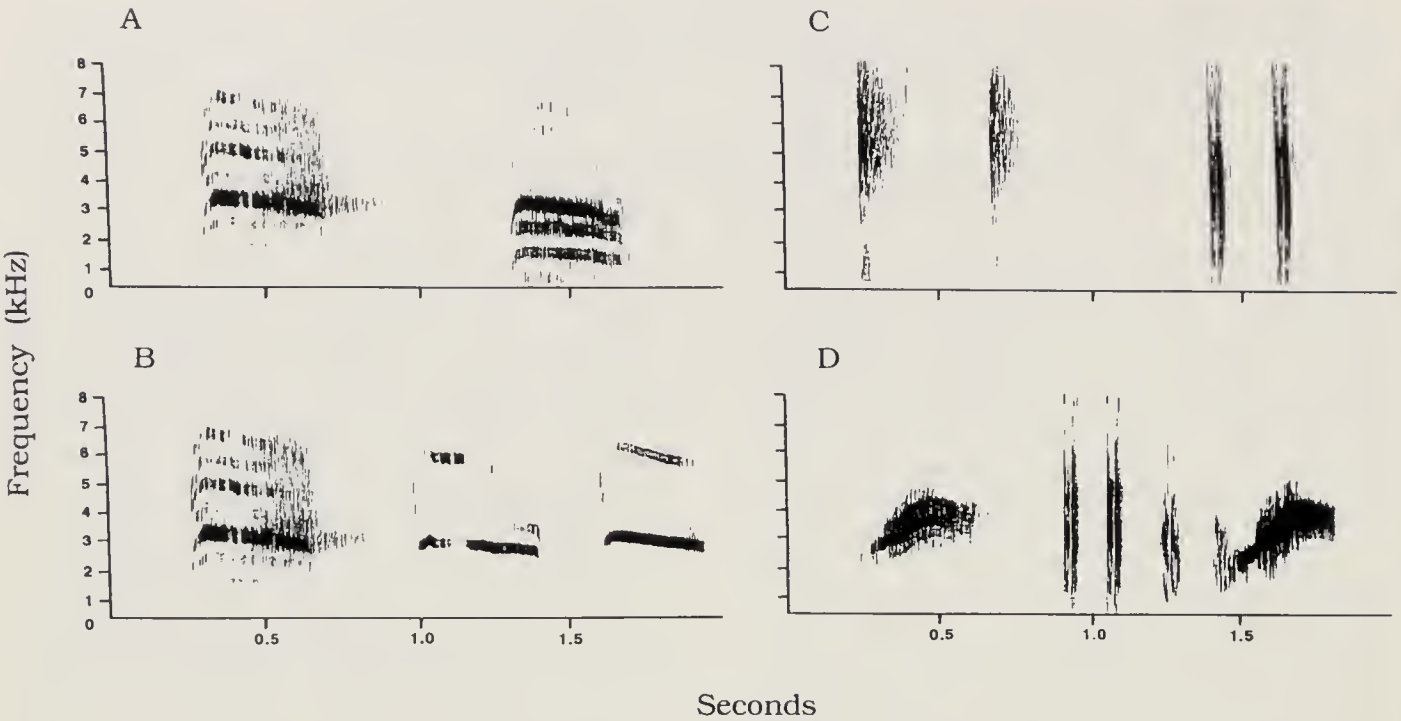

FIG. 1. Sound spectrograms of mimicked calls in the call repertoires of Eastern Towhees compared with corresponding calls in the repertoires of presumptive model species. A, right, mimicry of Jay call of towhee in New York (KFRS male), left, Jay call of Blue Jay (New York); B, right, two Jay-like mimicries of towhee in Texas, left, Jay call of Blue Jay (New York); C, right, thrasher-like calls of towhee in New York (FINS male), left, corresponding calls of Brown Thrasher (New York); D, Chewink calls and thrasher-like mimicries of FINS male in a representative portion of a mixed-call sequence. All recordings by the authors.

spectrograms were prepared on a Kay Elemetrics Sona-graph 7029A 5–16 kHz Spectrum Analyzer with a Krohn-Hite Model 3550 filter. Most calls from presumptive models were recorded in New York by the authors using the same equipment. Robin calls were obtained from the archives of the Borror Laboratory of Bioacoustics.

RESULTS

We documented call mimicry during the breeding season in six male towhees in three states. Presumptive heterospecific sound models of these birds were Blue Jay (*Cyanocitta cristata*), Brown Thrasher (*Toxostoma rufum*), and American Robin (*Turdus migratorius*).

Among these call mimickers, the Blue Jay's characteristic "Jay" call (Fig. 1A, B, left) was rendered in 4 of 7 cases. Three of these individuals (HMF, KFRS, and Texas) incorporated this call into their call repertoires without substitution. Another bird (FINS) used the alarm call of the Brown Thrasher (Fig. 1C, left) in the same manner. A male at Muttontown NP employed a Jay call in a prolonged, muted soliloquy that contained primary song elements and some species-typical calls. Comparisons of these calls from most of the birds mentioned with corresponding calls from the putative models are shown in Figure 1.

Three males (New Jersey, New York) mixed heterospecific and "Chewink" calls in the same bouts of alarm calling when disturbed. No bouts consisted of just one or the other call types. Heterospecific calls were uttered 1–3 times between "Chewink" calls or call sequences. The Kalbfleisch FRS male also exhibited a tendency to utter more jay-like calls during periods of intense (high calling rate) calling than during more "relaxed" periods (low calling rate). Another variation occurred during a bout of rapid calling near an active nest. The Kalbfleisch FRS male began by coupling the jay-like and "Chewink" calls into a single compound vocalization ("jeah-chwee . . .") in which a longer pause occurred between the jeah-chwee couplets than within them. Later in the same calling bout, as the rate of calling slowed, jeah and chwee calls were separated into single notes. In one period (165 s) of mixed calling, the Fire Island NS male uttered 54 mimicries (41.2%) and 77 Chewink calls. This towhee often rendered its mimicry in single or doubled versions ("tchap-tchap") in thrasher-like fashion.

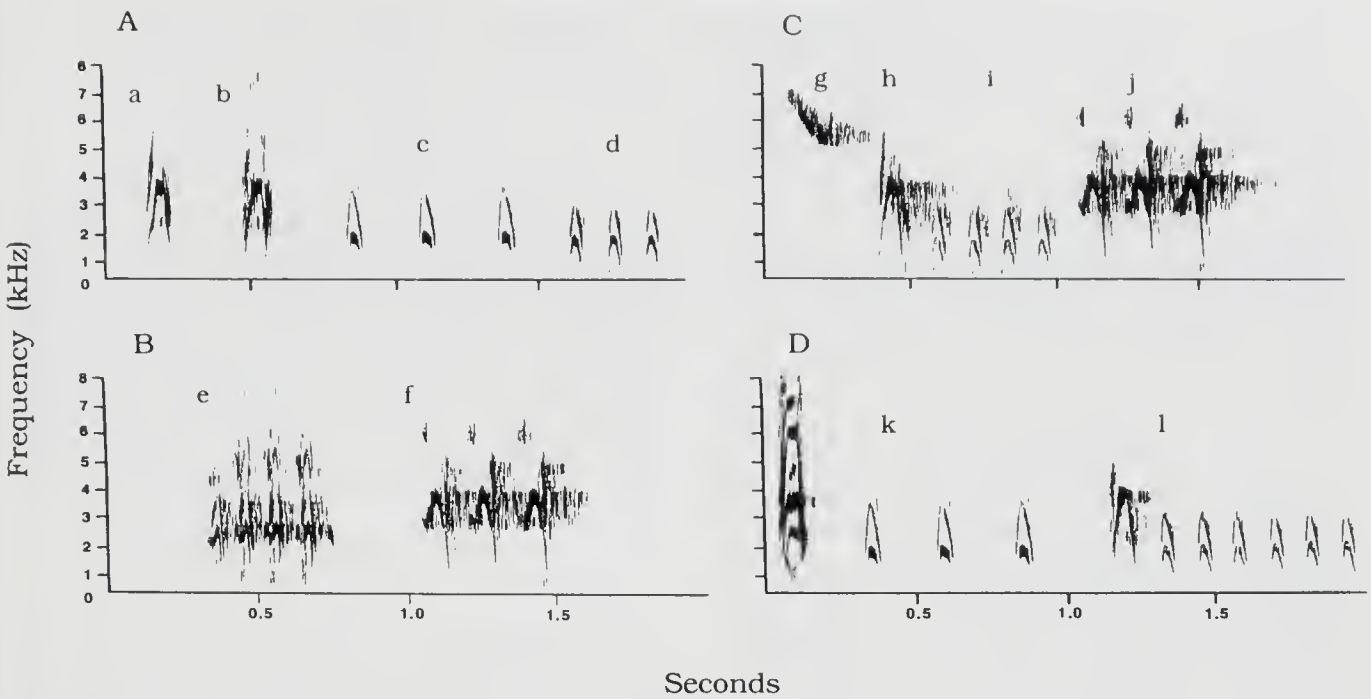

FIG. 2. Sound spectrograms of robin-like calls in the song repertoire of an Eastern Towhee in New York, compared with corresponding calls of American Robins. A, a, Stip! call of robin (BLB 13688), b, Stip! call of towhee (see text), c, Pup-chatter of robin (BLB 13688), d, Pup-chatter of towhee; B, e, Chee-whinny by robin (BLB 16350), f, Chee-whinny by towhee; C, towhee mimicry of robin call combination, used in song repertoire as a song-type [see stip! pup pup pup chee chee chee (g, h, i, j)]; and D k, Stip! pup pup pup combination of robin (BLB 13688), l, Stip! pup pup pup . . . combination of towhee.

The towhee observed in Texas exhibited still another mimetic variation. Its jay-like and Chewink calls were employed separately in different contexts. The jay-like call was the sole vocalization used in mobbing observers (CES, REB), while only the Chewink call was given after the towhee ceased mobbing and began foraging.

A color-banded (XR-GG) male present at Kalbfleisch FRS from 1965 (at least) to 1972 sang two distinctive song-types that incorporated sequences of three or four different robin-like calls as song elements. These calls are characterized as follows: (1) See-scream, a high-pitched squeal, seee (perhaps "sss" of Bent 1949; Fig. 2g), (2) Pup-chatter, a low-pitched, soft pup, repeated in a series (phrase) as pup-pup-pup . . . ("tut-tut . . ." syllables of Bent 1949; Fig. 2c, d), and (3) Chee-whinny, an insistent, loud chitter, performed as a short series of notes, e.g., "chee-chee-chee" ("each-each-each" of Bent 1949; Fig. 2e, f). A fourth call type, transliterated as "stee" ("stip"), is probably convergent on a robin-like call and is discussed below.

DISCUSSION

Our observations suggest that learning may play a role in the acquisition and use of certain calls by the Eastern Towhee. Some individuals expand their call repertoires by adding a mimicked sound, and others may employ sequences of mimicked calls as distinctive song types. Among individuals that employ such sounds in their call repertoires, variation in the temporal and contextual characteristics of novel call use in relation to the Chewink call is also noteworthy.

Several types of evidence support the view that mimicry of sounds from heterospecific models best explains most of our observations. (1) Hundreds of hours of observations yielded no evidence that unusual "nonmimicked" sounds (atypical calls that could not be matched to likely models) occur even rarely in towhee call repertoires. Rather, in each of the cases reported here, an unexpected call was rendered by towhees in widely separated geographic settings that corresponded to a distinctive sound employed otherwise only by another species. (2) These unusual and unlikely sounds were remarkably similar in sound "quality" to their heterospecific analogues. Also, there are no sounds in the normal call repertoire of the Eastern Towhee that even closely resemble in sound structure the

jay-like or thrasher-like sounds uttered by the call mimics (Greenlaw, unpubl. data). (3) The presumptive models were characteristic faunal neighbors of the towhees. Consequently, we regard these uncharacteristic towhee sounds as evidence of call mimicries. As such, they represent distinctive "markers" that implicate some learning in the development of call use in call and song repertoires in Eastern Towhees.

The use of robin-like calls in two song-types sung by XR-GG deserves special comment. The "stee!" or "stip!" element was widely represented in the song repertoires of Long Island towhees (Ewert 1978: fig. 11V, appendix 2). Thus, this element was probably copied from other towhees, or improvised, and is convergent on the similar robin's call (Fig. 2, a vs b). The other robin-like elements were unique to XR-GG. Yet, regardless of origin, both mimicked and convergent notes were uttered by XR-GG as components of songs in the same sequences commonly heard in nonsong contexts in American Robins (JSG, pers. obs.; Fig. 2D). This may mean that the unit of mimicry was a call complex, not individual calls that were later assembled into a robin-like sequence.

Little is known about vocal development in Eastern Towhees. Song sharing is well known among immediate neighbors in towhee populations (Greenlaw 1996). Also, nestling towhees that were isolated from wild populations failed to develop the familiar Chewink call. Rather, they use abrupt, atypical notes that bear little resemblance to this call (Ewert 1979; R. E. Ball, pers. comm.). Our observations suggest that call mimicries may express themselves in adulthood either in call repertoires (simple call mimicry) or in song repertoires (mimicry of heterospecific call complex, or a sound "template" that allows assembling mimicked call units into a complex sequence).

This report of call mimicry in Eastern Towhees suggests that sound or social experience may play some role in the development of call repertoires in this species, and in the specific use of mimicked calls in generalized "alarm" contexts. The hypothesis that calls in songbirds are "genetically fixed" (strictly maturational; e.g., Lanyon 1960) needs to be examined using isolation and tutoring experiments on a case by case basis.

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Display Behavior of Male Sprague's Pipits

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ABSTRACT.—Male aerial territorial displays of Sprague's Pipits (*Anthus spragueii*) are described in detail for the first time. Aerial displays were performed primarily in the morning, with four males' average display rates ranging from 11.8–34.8 min. One male displayed continuously for 3 hrs; no other passerine has been documented to have such prolonged aerial displays. Display flight energetics were estimated with implications explored. *Received 6 March 1997, accepted 17 March 1998.*

Among the least known resident North American passerines is the Sprague's Pipit (*Anthus spragueii*). The dearth of information on this species is not surprising given its highly cryptic plumage and habits. In fact, even territorial males' persistent and relatively conspicuous flight display have never been described in detail. Here, I present the first information on male display rates and energetics of Sprague's Pipit.

STUDY AREA AND METHODS

Territorial males were studied during 15–20 June 1995 and 20–23 May 1996, just north of Thompson Lake, Lostwood National Wildlife Refuge, Burke County, North Dakota. This location is precisely where Green (1992) censused annually breeding grassland passerine species, including Sprague's Pipits, during 1987–1990. The study site is rolling, mixed grass prairie (*Stipa* spp., *Agropyron* spp.), interspersed with small seasonal wetlands, in the Missouri Coteau physiographic region (Green 1992). The study area was prescribe-burned on 14 August 1980, 8 August 1982, 9 July 1985, and 15 May 1992. More than 90% of above ground plant growth and litter was eliminated in the burns (Green 1992; K. Smith, pers. comm.).

Territorial males were not marked in 1995; however, the sex of birds studied was confirmed by collection at the end of the observation period. In 1996, three territorial males were captured with mist-nets using a study skin as a lure. A recording of flight display calls was played from the grass beneath the lure. Captured males were color-marked on the lower abdomen with a non-toxic, permanent ink marker ("Magic Marker" by Binney & Smith Inc., Easton, PA). This ink wears off within a week or two, leaving the bird unharmed (pers. obs.). In this paper, "T" followed by a number is used to designate 1995 territorial males, and initials refer to 1996 color marked territorial males. Total number of observation hours were: May (24.75 morning, 6.5 afternoon), June (24.5 morning, 10.0 afternoon). Contiguous territorial male display rates were simultaneously quantified on several occasions, hence the hourly totals of individual males under Display Rate section exceed the above totals.

Observations of displaying males were made from the periphery of each display area. The following parameters were recorded: number of display calls, number of wing beats between display calls, duration of display, wind speed and direction, and temperature. A stopwatch was used to quantify aspects of the display flight. Limited tape recordings were made of displaying males with Sony TCM- 5000EV and Sony TC-D5Pro II cassette recorders, and Sennheiser ME 80 and ME 66 microphones.

Estimates of display flight energetics were calculated using Pennycuick's (1989) computer software program (Program # 1). Flight speed used in predicting energy expenditure of flight by Program # 1 was zero. Mass ($\bar{x}$ = 23.5 g) and wing span ($\bar{x}$ = 255 mm) were measured from two territorial males (KU 87231-2) before preparation. Hourly windspeed data were obtained from Lostwood N.W.R. headquarters (681 m in elevation), about 2 km from the study area.

RESULTS

Males were not uniformily distributed through the study area; all territorities were located in elevated areas with short grass and relatively low sedge and forb (mainly Asteraceae) densities. Highest male densities were along a north–south oriented ridge that separated two seasonal, shallow wetlands. Along this ridge's steepest section (ca 710 m in length), five males held territories in 1995; at least three were present in 1996. All three 1996 territorial display arenas were in sites where males had been removed in 1995. In 1995, five other territorial males were present along ridgetops with similar vegetation characteristics of a broad rolling area to the south. Because of low display rates, it was unclear how many territorial males occupied the southern area in 1996.

Displays were simple but often prolonged. Males took advantage of the almost ever-present wind by flying from the ground into the wind until they were from 50 to over 100 m

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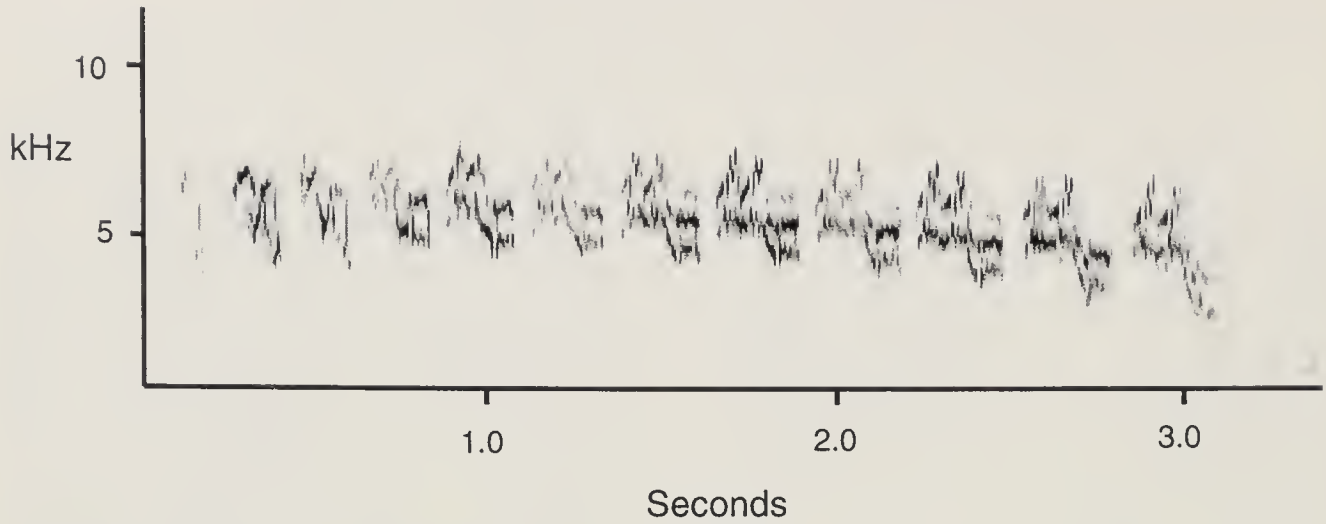

FIG. 1. Spectrogram of flight display song of a territorial male Sprague's Pipit (*Anthus spragueii*).

above the ground. Displays were limited to a relatively small area ($\bar{x}$ = 61.3 × 55 m; n = 3). The males invariably flew into the wind, while constantly flapping their wings until they gave the 7–12 syllable display song. This song is a thin, relatively high pitched "tzsee-tzsee-tzsee-tzsee-tzsee-tzeee-tzeee", of 2.5–3.0 sec duration (Fig. 1). As can be seen in the spectrogram (Fig. 1), the syllables are complex in structure, appearing as harmonics that modulate in frequency. Simultaneously with beginning the display song, the wings were extended parallel to the body, and the bird entered a glide for the duration of the song. When in the glide, males were displaced backward by wind; however, they did not appear to drop much in altitude. Terminating the song, males resumed flapping until the next song. Wing beats between songs varied considerably, ranging from 7-27 beats. Wind speed did not appear to affect wing-beat interval (# of wing beats between display songs). For example, during one of the windiest observation periods ($\bar{x}$ = 29.4 km/h), T1 averaged 14.5 wing beats between songs, whereas the same individual averaged 17.5 wingbeats in a 20.3 km/h wind, and 10.9 wing beats in a 24.6 km/h wind.

At the end of each display bout (defined as uninterrupted display) males either folded their wings and dropped directly to the ground within the display area, or they chased other pipits that had entered the display area. On one occasion, male T1 interrupted its display to chase an adult male Chestnut-collared Longspur (*Calcarius ornatus*) that flew across his territory. Males were never observed singing on or near the ground.

The frequency and duration of display bouts and the frequency of songs per bout varied considerably within and among males and between years, with displays concentrated in the morning. Territorial males displayed less in May 1996 than in June 1995. In May, male BK's longest display bout was 32 min (7.3 songs/min), and RD's was 41 min (7.0 songs/min). These display rates were the highest per bout. However, although highest display rates/min were recorded in May, duration of bouts was greater in June. In May males BK and RD averaged morning display bouts of 12.3 min (13.75 h; n = 3 mornings) and 11.8 min (15.25 h; n = 4 mornings) respectively, whereas in June T1 and T2 averaged 16.9 min (11.2 h; n = 3 mornings) and 34.8 min (8.75 h of obs. on 3 mornings) respectively. On 19 June, T2 displayed continuously for 2 hr 59 min (5.7 songs/min). A nearby male, T1, displayed for as much as 1 h 13 min (6.01 calls/min) in a single bout.

Afternoon displays were generally rare. No displays were recorded during 6.5 h of afternoon observation in May 1996. Only one male displayed during a total of 10.0 h of June afternoon observation. On 15 June, T1 displayed from at least 17:00 C.S.T. until 20:00, with only two breaks of 8 and 3 min each. During this period, he called 806 times (4.5 songs/min). During an additional 8 h of observation over the next two afternoons (15:50–19:45), he was heard singing only a few times during one 15 min period. Based on

minimal display rates, males do not appear to take advantage of thermal activity which increases in the afternoon with temperature.

Display in male pipits is presumed to involve high energy expenditures because of the high costs of flight (Pennycuick 1989). Average headwinds during 17:00–20:00 on 15 June while male T1 displayed was 20.3 km/h (5.67 m/sec). Pennycuick's (1989) model predicted that the minimum power speed (V_{mp}) for displaying males was 5.9 m/sec, and that maximum range speed (V_{mr}) was 10.4 m/sec. V_{mp} was the air speed at which the least amount of work was done (or fuel consumed) per unit time. V_{mr} was the air speed at which the least amount of energy was expended per unit distance. Estimated fat consumption for flight display at V_{mp} [1.7 W for chemical power, 3.9×10^7 J/kg for energy density of fat (Pennycuick 1989)] was 0.157 g/h. Thus, a male at this site displaying under the above climatic conditions for three consecutive hours (n = 2.63 h of constant flapping; an average of 2.3 sec were subtracted for each song/glide) would expend an estimated 0.41 grams of fat, or 1.8% of its body mass ($\bar{x}$ = 22.8 g ± 0.2 SE; n = 4). Although all four territorial males that were collected had only light amounts of fat, I did not quantify what percent fat reserves comprised the total body mass. In small nonmigrating birds, 3–5% of the body mass is fat (Gill 1990), thus the above estimate for fat expenditure for a three hour display would result in consumption of about 40% to nearly 60% of a male pipit's fat reserve.

DISCUSSION

No other passerine has been documented to have such prolonged aerial displays. Maximum continuous male display of the renowned Skylark (*Alauda arvensis*) is 68 min (Rollin 1943), and unpaired males of the Woodlark (*Lullula arborea*) have been recorded performing displays of 70–90 min (Mackowicz 1970). Skylark display bouts average 2.0–2.5 min (Cramp 1988) to about 4 min (Hedenström 1995), and Woodlark song bouts usually last about 2 min (Mackowicz 1970). No Old World *Anthus* is known to have extended aerial displays (Cramp 1988), and the only species that comes close is the Short-billed Pipit (*Anthus furcatus*) of southern South America. One male *A. furcatus* was recorded singing continuously for 55 min before it dove to the ground after tape playback (Belton 1985). Interestingly, this pipit has been suggested as the closest relative of Sprague's Pipit (Hall 1961, Ridgely and Tudor 1989).

Although Sprague's Pipit display bouts are prolonged, display behavior appears to be limited to a few weeks (Coues 1874; R. Murphy and K. Smith, pers. comm.). Murphy and Smith (pers. comm.) have noted persistent male display from the time of arrival (third week of April) through the third week of May at Lostwood NWR, followed by a period of two to three weeks where display rates are reduced, followed by another period of elevated display rates. I would hypothesize that this bimodal display regime is related to the breeding cycle, with display rates decreasing once a first clutch of eggs is laid and copulation opportunities decrease. A similar cycle has been widely documented in the Motacillidae and many other passerines (Cramp 1988). The second period of elevated display rates may coincide with onset of replacement broods or initiation of second broods. Because of differential nesting success, male display rates should become less synchronized as the season progresses.

The available data seem to support this hypothesis. The median date of clutch initiation near Kyle, Saskatchewan, Canada, about 500 km northwest of Lostwood, was 8 June (Mahr 1973); however, this figure is based on pooling all nests. This undoubtedly included failed first attempts as well as second broods. Seventeen nests located during the last 20 days of May (no nests were located during the first 10 day period) probably best exemplify first-clutch initiation dates in southwestern Saskatchewan; mean incubation and nestling periods were 14 days and 11 days, respectively, with 50% of pipits fledgling between late June and mid-July (Mahr 1973). Mahr (1973), working with unmarked birds, estimated an average of 1.5 broods yearly for this species at Kyle, Saskatchewan. At the same locality, Sutter et al. (1996), using radio telemetry, documented at least one example of a second brood: a female that initiated a second nest 21 days after her first clutch fledged.

My observations of display rates coincide with these periods. Perhaps lower display

rates recorded in May 1996 compared with June 1995 resulted from birds having just completed egg laying in May. I located a nest with 5 eggs (a complete clutch) on 22 May in RD's territory. During the third week of June, birds may have been in the final stage of the first brood, and preparing for second broods. I flushed one presumed female carrying food during this period.

Given that flight is energetically very costly (Pennycuick 1989), males should be minimizing energy expediture and maximizing vocal transmission by displaying when wind conditions are optimal. From an energetic standpoint males should display at or near the minimum power speed $V_{mp.}$ the speed with minimum energy cost (Pennycuick 1989). Indeed, during male T1's marathon display period, 17:00–20:00 on 15 June, the wind was an average of 5.6 m/sec and the estimated V_{mp} was 5.9 m/sec. Hedenström and Alerstam (1996) demonstrated that a Skylark's (*Alauda arvensis*) average airspeed during horizontal song flight displays did not differ significantly from the predicted $V_{mp.}$

Theoretically, maximal sound transmission in grassland environments should be at dawn when daylight wind perturbance is least (Morton 1975, Henwood and Fabrick 1979). Unlike all the other grassland passerines at Lostwood, male Sprague's Pipits rarely displayed at first light; they typically were not heard until after 04:30, over 30 min after dawn. Males may need to obtain some food resources and for the wind to approach V_{mp} before they begin extended displays. Detailed analyses of the energetics of this pipit's display will need to incorporate a number of biotic and abiotic factors to determine more precisely what parameters best explain temporal occurrence and duration of pipit displays.

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Effects of Microsite Selection on Predation of Artificial Ground Nests

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ABSTRACT.—We studied the effects of microsite selection on depredation of artificial ground nests in central Pennsylvania from May–July 1996. Our objectives were to compare depredation of artificial ground nests in relation to the type of structure (tree vs log) adjacent to a nest and the direction (north vs south) of a nest from the structure. Sixty nests were placed in each of five trials with 20 nests each placed in contiguous forest, forested patch, and forested corridor habitats. Eighty-eight (29%) of the 300 artificial nests were disturbed during five trials. The number of disturbed nests did not significantly vary ($P > 0.05$) with time period (trial). Nest fate differed significantly among the three habitats ($P = 0.001$), with 20%, 43%, and 25% of the nests disturbed in the contiguous forest, forested patch, and forested corridor habitats, respectively. These rates of nest predation corresponded to those reported in previous studies of artificial ground nests at the same study site in central Pennsylvania. Nest fate was not associated with the type of structure at the nest site ($P > 0.05$) or with the direction of the nest from the structure ($P > 0.05$). We conclude that neither the type of ground-level structure near which artificial ground nests are placed nor the direction of nests from these structures influences nest fate. *Received 2 Dec. 1997, accepted 17 April 1998.*

Artificial nest studies have shown experimentally that avian nesting success declines with reduced forest size or with greater forest fragmentation (e.g., Wilcove 1985, Yahner and Scott 1988, Yahner et al. 1993, Yahner and Mahan 1996a). Previous studies also have shown that depredation of artificial nests may vary with time of placement during the season, degree of concealment provided by vegetation surrounding the nest site, and color of eggs used in artificial nests (Sugden and Beyersbergen 1986, Yahner and Wright 1985, Yahner and Mahan 1996b). Yahner and Voytko (1989) observed that depredation of artificial aboveground nests placed at random sites did not differ ($P > 0.05$) from nests placed at sites used by birds the previous breeding season. Yahner and Mahan (1996b) recommended the use of brown chicken eggs to simulate nests of Ruffed Grouse (*Bonasa umbellus*) and Wild Turkey (*Meleagris gallopavo*) in artificial nest studies. Investigators of these types of ground nests typically place a small clutch of brown chicken eggs in a slight depression adjacent to a large tree or log (e.g., Yahner and Wright 1985, Yahner et al. 1993). However, the effects of microsite selection for placement of artificial ground nests have not been examined to our knowledge. Our objectives were to compare predation of artificial ground nests in relation to the type of structure (tree vs log) adjacent to a nest and the direction (north vs south) of a nest from the structure.

STUDY AREA AND METHODS

We conducted our study at the 1166-ha Barrens Grouse Habitat Management Area (HMA), State Game Lands 176, Centre County, Pennsylvania, which has been the location of several previous studies on artificial ground nests (e.g., Yahner and Wright 1985; Yahner et al. 1993; Yahner and Mahan 1996a, b). The Pennsylvania Game Commission has created habitat for Ruffed Grouse at the study area since 1976 using an even-aged system of forest clearcutting (see details in Yahner 1993, Yahner et al. 1993). The Barrens Grouse HMA contains a sector reference and a treated sector of similar size. The reference sector is uncut and is termed the contiguous forest habitat. The treated sector is divided into forested patch and forested corridor habitats (Yahner 1993, 1997).

Forest in the reference sector, in uncut plots of both forested patch and forested corridor habitats, and adjacent to the Barrens Grouse HMA, has not been cut for approximately 75–80 years. Principal overstory trees (woody stem > 7.5 cm dbh and > 1.5 m tall) on each sector were white oak (*Quercus alba*), northern red oak (*Q. rubra*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), red maple (*Acer rubrum*), quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), and pitch pine (*Pinus rigida*; Yahner 1993, 1997). Major understory trees (woody stem = 2.5–7.5 cm dbh and > 1.5 m tall) and tall shrubs (woody stems < 2.5 cm dbh and > 1.5 m tall) included oak, red maple, aspen, and black cherry (*Prunus serotina*).

The treated sector contained 136 contiguous 4-ha blocks; each block consisted of four 1-ha (100 × 100 m) plots arranged in a clockwise pattern (plots A–D; Yahner 1993, 1997). In each block of the forested patch habitat, only plot D was uncut, whereas plot A was clearcut in winter 1976–1977, plot B in winter 1980–1981, and plot C in winters 1985–1986 and

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TABLE 1. Fate of 300 artificial ground nests in relation to time period, habitat, type of structure adjacent to the nest, and direction of the nest from the structure at the Barrens Grouse Habitat Management Area, Centre County, Pennsylvania, 1996.

		Nest fate			
		Undisturbed		Disturbed	
Variable	Level	*n*	%	*n*	%
Time period	Trial 1	40	67	20	33
	Trial 2	46	77	14	23
	Trial 3	47	78	13	22
	Trial 4	45	75	15	25
	Trial 5	34	57	26	43
Habitat	Contiguous forest	80	80	20	20
	Forested patch	75	75	25	25
	Forested corridor	57	57	43	43
Structure type	Tree	107	70	46	30
	Log	105	71	42	29
Nest direction	North	108	68	51	32
	South	104	74	37	26

1986–1987. In the forested corridor habitat, both plots C and D were uncut, but plot A was clearcut in winter 1976–1977, and plot B was cut in winters 1985–1986 and 1986–1987. Thus, the forested patch habitat gave a checkerboard pattern of cut plots (A–C) and uncut plots (D), whereas the forested corridor habitat consisted of alternating strips of cut plots (A and B) and uncut plots (C and D).

Ruffed Grouse and Wild Turkey were common gallinaceous birds nesting at ground level at the Barrens Grouse HMA; potential predators on nests of these species included American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Virginia opossum (*Didelphis virginianus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), black bear (*Ursus americanus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*) and snakes (Therres 1982, Yahner and Mahan 1996b).

We placed artificial ground nests during five time periods (trials) from late May through late July 1996 (Table 1). A nest contained three fresh, brown chicken eggs and was put in a slight depression immediately adjacent (nearest egg approximately 3 cm away) to the nearest ground-level structure (tree or log ≥ 15 cm diam) and either north or south of the structure (after Yahner and Wright 1985, Yahner et al. 1993). Brown chicken eggs were used to simulate the contents of actual nests of grouse or turkey (Yahner and Mahan 1996b).

Each trial was six days, and eight days elapsed between trials (Yahner and Scott 1988, Yahner et al. 1993). During a trial, 20 random sites for nest placement were selected for nest placement in the contiguous-forest habitat; 20 uncut plots (plot D) were also randomly selected for nest placement in both forested patch and forested corridor habitats. This experimental design gave a total of 300 nests (Klett and Johnson 1982) which were randomly placed for each trial and habitat at one of four types of sites: north of a tree, north of a log, south of a tree, or south of a log. Nest sites in the forested corridor habitat were at least 50 m from a disturbance (e.g., logging road); nest sites in the other two habitats were placed approximately 50 m from an edge in the center of plot D. Rubber gloves and boots were worn to reduce human scent when placing nests (Nol and Brooks 1982).

We determined the fate (undisturbed or disturbed) of nests six days after placement between 07:00 and 13:00 (EST). A nest was disturbed if at least one egg was broken or missing. Appearance and mode of disturbance of eggs were used occasionally to identify the type of predator, e.g., peck holes in eggs often were characteristic of avian predators (Rearden 1951, Yahner and Wright 1985). Eggs and egg fragments were removed at the end of each trial.

We examined the dependency of nest fate (undisturbed vs disturbed), time period (trials 1–5), habitat (contiguous forest, forested patch, and forested corridor), type of structure at the nest site (tree vs log), and direction of eggs from structure (north vs south), using a five-way test-of-independence (BMDP4F, Dixon 1990). Interactions of nest fate with the other variables were tested with likelihood ratios (G^2) based on log-linear models, which are suitable when analyzing attribute data in multi-way contingency tables (Dixon 1990, Sokal and Rohlf 1995). We used *a posteriori G*-tests for goodness-of-fit about the cells (levels) of interest if nest fate was significantly dependent on a given variable (Sokal and Rohlf 1995). All statistical analyses were performed using BMDP4F software on an IBM/CMS computer.

RESULTS

Eighty-eight (29%) of the 300 artificial ground nests were disturbed during the five trials (Table 1). Of these disturbed nests, only nine (10%) were attributed to avian predators;

the identity of predators on the remaining disturbed nests was unknown. The number of disturbed nests did not vary significantly ($P > 0.05$) with time period, ranging from 22–43% of nests disturbed per trial. More nests were disturbed in the forested patch habitat (43%) than in either the contiguous forest (20%) or forested corridor habitats (25%). The number of disturbed nests in the forested patch habitat was significantly higher than expected compared to either the forested corridor or contiguous forest habitats (all G values ≥ 4.8, df = 1, $P < 0.05$); however, the number of disturbed nests was similar ($P > 0.05$) between forested corridor and contiguous forest habitats.

Nest fate was not associated with the type of structure at the nest site ($P > 0.05$), the direction of the nest from the structure ($P > 0.05$), or with interactions of two other variables (i.e., time period and habitat) considered simultaneously (all $P > 0.05$). Forty-six (30%) of the nests adjacent to trees were disturbed compared to 42 (29%) nests near logs. Fifty-one (32%) of the nests placed north of a structure were disturbed compared to 37 (26%) of the nests located south of a structure.

DISCUSSION

Our finding that 29% of the artificial ground nests were disturbed during the study corresponds to rates of disturbance noted in previous studies of artificial ground nests using brown chicken eggs at the Barrens Grouse HMA (22–42%: Yahner et al. 1993; Yahner and Mahan 1996a, 1996b) or to predation rates on ground nests of Spruce Grouse (*Canachites canadensis*; 17–70%: Redmond et al. 1982). Moreover, as in a previous study subsequent to clearcutting in winters 1985–1986 and 1986–1987 (third cutting cycle) at the study area, avian predation on artificial ground nests has continued to be low (9%) compared to the pre-1985 era when avian predation tended to be higher (36%; see discussion by Yahner et al. 1993). Also, as in recent studies at the Barrens Grouse HMA, numbers of disturbed nests did not significantly differ among trials (Yahner et al. 1993, Yahner and Mahan 1996a).

Our finding that nests in the forested patch habitat were more likely to be disturbed than nests in either the contiguous forest or forested corridor habitats has been documented in previous studies of artificial ground nests (Yahner and Mahan 1996a), artificial aboveground nests (Yahner and Mahan, unpubl. data), and actual nests of Wood Thrush (*Hylocichla mustelina*; Yahner and Ross 1995) at the Barrens Grouse HMA. Yahner and Mahan (1996a) concluded that higher rates of nest predation in small uncut forest patches than elsewhere was perhaps the result of both greater amounts of forest edge and greater foraging success by predators in uncut plots in the forested patch habitat. Edge species, e.g., raccoons and American Crows, probably also foraged disproportionately more in the small forested patches than in the contiguous forest or forested corridors (Yahner and Mahan 1997).

The major result of our study, which has implications on the experimental design of studies using artificial ground nests, is that depredation did not vary with respect to microsite features. We expected *a priori* that nests proximal to logs or those placed south of a ground-level structure would be more susceptible to visually foraging predators, such as corvids that forage during the day, than those placed near trees or in a northerly direction (e.g., Yahner and Wright 1985). A nest next to logs, for instance, presumably would be detected more readily from above the nest than a nest adjacent to an overstory tree. Furthermore, with the sun moving from east-to-west in the southerly sky above the forest canopy, a nest placed in a northerly direction from a structure would be better shaded and, hence, possibly better concealed from visually oriented predators than a southerly nest.

In conclusion, we believe that the type of ground-level structure near which artificial ground nests are placed or direction of nests from these structures will not have a major influence on nest fate provided that nests are within a reasonable distance (nearest egg approximately 3 cm away) from a relatively large ground-level structure ($\geq$ 15 cm diam).

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Ornithological Literature

Edited by William E. Davis, Jr.

A BIRDER'S GUIDE TO VIRGINIA. Compiled by David W. Johnston. American Birding Association, Inc., Colorado Springs, Colorado. 1997: 280 pp., 46 maps, 10 black-and-white photographs, 13 line drawings. $18.95 (soft wrap-around cover, wire-O binding).—Another in the burgeoning series of American Birding Association bird finding guides, this book generally follows the format of previous volumes except that the bar-graphs of most books are replaced by an annotated list of 425 species (390 of which occur regularly in the state). The introductory materials include a brief review of the geology and physiography of the state; a section on ornithological history; weather and seasonal variations; tick, chigger, and other pest warnings; where to stay; who to write to for maps and other information; and some birding opportunities of special interest such as the annual Eastern Shore Birding Festival. The site guide section divides the state into six regions, Eastern Shore, Coastal Plain, Northern, Central, and Southern Piedmont, and Southern Mountains and Valleys. Each section begins with a brief description of the region and a regional map, followed by site guides (some are divided into subsections) each of which has a map and text. The text is divided into sections on background, essentials, habitats, birds (season by season), rare or unusual birds, and special comments. The special comments sections are particularly useful, often describing non-birds of interest such as wildflowers, mammals, or reptiles, and areas where tape recorders should not be used. A chapter on hawk-watching (including a bar graph and site map), and a chapter on pelagic birding will be of special interest to many. In the annotated checklist asterisks denote Virginia specialty birds, which are treated in a separate chapter. The chapter on other animals of Virginia lists butterflies, amphibians, reptiles, and mammals together with brief comments on status and distribution, and should be of interest to those with natural history interests that go beyond birds. The book is, as is usual for this series, well designed, well edited, and user friendly. I found the site descriptions excellent for the areas of the state I know best, and assume the rest are equally good. I highly recommend this book to anyone planning to visit Virginia.—WILLIAM E. DAVIS, JR.

THE FOOD WEB OF A TROPICAL RAIN FOREST. Edited by Douglas P. Reagan and Robert B. Waide. Univ. of Chicago Press, Chicago, Illinois. 1996: 616 pp., black-and-white photographs with caption figs., numerous tables. $39.95 (paper); $110.00 (cloth).—This multi-authored volume represents an ambitious and successful attempt to provide a comprehensive analysis of the trophic dynamics of a single tropical rain forest. However, the rain forest chosen is El Verde, at an elevation between 300 and 500 meters on the northwest slope of the Luquillo Mountains on the island of Puerto Rico. Situated as it is, on an island, this forest is dramatically different in species richness and thus in trophic complexity from any mainland rain forest in Central or South America. Thus it becomes difficult to draw any generalizations from this otherwise model study. The book is divided into 14 chapters, of which one, authored by Robert B. Waide, is on birds. Birds therefore occupy about 7% of the total pages in the book, although birds are occasionally mentioned in other chapters.

Though birds exert significant influences at many points on the food web of El Verde, they are most influential as predators, particularly on lizards and frogs. Other trophic influences, such as nectarivory and frugivory are also important avian contributions to the overall trophic dynamics, especially with regard to dispersal of plants. The overall ecological importance of birds in part is due to the absence of many kinds of mammals that are important seed dispersers in mainland forests. Avian

species richness is far lower in El Verde than on mainland forests, a factor that permits greater ease of analysis but which makes the resulting analysis unique to this ecosystem. There are only 30 common species at El Verde, 8 of which are endemic to Puerto Rico and the Virgin Islands. This represents a strong distinction between El Verde compared with mainland communities, where rare species make up a major component of the avifauna. Biomass of birds at El Verde compares closely with that of mainland communities, however. Although there are fewer species, the number of birds per hectare is essentially equal to that found typically in mainland communities. Wintering migrant species (nine wood warbler species) have an important functional role in the El Verde as insectivores, though none is particularly abundant.

The chapter on birds represents an excellent attempt to understand the trophic dynamics of bird communities. This book, as a whole, is an important contribution to the study of Neotropical ecology.—JOHN C. KRICHER.

A GUIDE TO THE BIRDS OF THE GALAPAGOS ISLANDS. By Isabel Castro and Antonia Phillips, with a foreword by Peter R. Grant. Princeton Univ. Press, Princeton, New Jersey. 1996: 144 pp., 32 color plates plus 30 black-and-white illustrations, 1 map. $24.95, cloth.—The Galapagos Archipelago is one of the most visited ecotourist destinations and it is timely that an updated bird guide becomes available. The Galapagos avifauna, though limited in diversity, is nonetheless unique in the ease by which most species can be observed and in its significance, particularly of the Geospizinae, to evolutionary biology. Most bird species that breed on the islands are not difficult to identify. Only one group, the Darwin's finches, poses significant field problems. This guide provides an adequate species account for each regularly occurring and many rarely occurring species, including status (migrant or resident), identification, distribution among islands (essential, as there is much by way of island to island differences), food, breeding behavior, and voice. It has interesting information on conservation status and it provides a useful though brief introduction to the islands, island ecosystems, climate, and conservation concerns.

Most field guides rely heavily on the plates and the quality of the color plates in this volume is weak. The species illustrated are not cross-referenced to the text, though the text does identify on which plate the species is illustrated. While most species are identifiable from the illustration on the plate, one longs for a good comparative plate of the Darwin's finches, accurately drawn, showing variability in bill size within a species. The illustrations provided on the plates are far short of this mark and will not be very useful in dealing with this group. Another problem with the plates is that very rare species are illustrated along with regularly occurring species. It may have been more useful to separate really rare species (such as ones for which there exists but a single record) from those which one sees almost daily. The black-and-white illustrations in the text are nonessential but pleasing.

The map of the islands does not include some of the more remote islands that, while they are not normally visited in most tours, are nonetheless mentioned in the text in various species accounts. The bibliography is useful in taking readers into the scientific literature. A bird species check-list is included.—JOHN C. KRICHER.

MIGRATORY SHORE AND UPLAND GAME BIRD MANAGEMENT IN NORTH AMERICA. 1994 (second printing 1995). T. C. Tacha and C. E. Braun. International Association of Fish and Wildlife Agencies, Washington, D.C. 223 pp., hardcover, 14 sepia-toned plates, numerous black-and-white photographs and range maps. Available free from the Caesar Kleberg Wildlife Research Institute, Campus Box 218, Texas A & M University-Kingsville, Kingsville, Texas 78363.—This volume is an update of the "Management of Migratory Shore and Upland Game Birds in North America (1977, International Association of Fish and Wildlife Agencies). It differs from that volume in that only game species have been included and the accounts have been written by primary authors (who selected their own coauthors) rather than by appointed committees. New art-

work by Don Radovich includes a full page sepia-toned portrait of each species in a preferred habitat. The artwork is pleasing and informative, adding much to the "class" of the book, although the color rendering differs substantially from the original artwork which I had an opportunity to see.

The book begins with an introductory chapter (K. M. Babcock) and ends with a summary chapter (Migratory Shore and Upland Game Bird Resources—Status and Trends, by T. C. Tacha, C. E. Braun, and R. E. Tomlinson). In between are chapters on fourteen species with one to five authors per account: Mourning Dove (*Zenaida macroura*), White-winged Dove (*Z. asiatica*), White-tipped Dove (*Leptotila verreauxi*), Band-tailed Pigeon (*Columba fasciata*), Sandhill Crane (*Grus canadensis*), American Woodcock (*Scolopax minor*), Common Snipe (*Gallinago gallinago*), American Coot (*Fulica americana*), Common Moorhen (*Gallinula chloropus*), Purple Gallinule (*Porphyrula martinica*), Clapper Rail (*Rallus longirostris*), King Rail (*R. elegans*), Virginia Rail (*R. limicola*), and Sora (*Porzana carolina*).

Each chapter stands on its own, being written in journal style and including an independent literature cited section. Chapters begin with a description of the species, a review of its behavioral ecology and habitats, its distribution and abundance, including discussion of census techniques and population trends, and data on hunting pressures and other sources of mortality. Each account includes a range map showing at least breeding and wintering distribution. Some accounts provide additional maps delimiting special management units (Mourning Doves), breeding bird survey and other census data, migration routes, and other information. Sections on management and research needs, included in each chapter, provide challenges for the next generation of wildlife biologists.

As its predecessor was, this volume will certainly be a valuable reference for gamebird biologists and managers, providing good reviews and useful bibliographies. Especially useful is the material related to the responses of populations to hunting pressures, habitat changes, and climate.—JEROME A. JACKSON.

THE RAVEN. By Derek Ratcliffe. T. & A. D. Poyser Ltd., England. 1997: xviii + 326 pp., 39 black-and-white photographs, 28 pen and ink illustrations (by Chris Rose), 18 figures, 27 tables, 5 appendices. $39.50 (cloth).—To my knowledge there is no better book on the Northern Raven. This is a remarkably comprehensive treatment of the species, particularly for a book of its moderate length. It is also a great companion to the author's previous book, *The Peregrine Falcon,* first published in 1980 and now in its second edition (1993). In fact, Ratcliffe notes that "The two species were conveniently studied together . . . where there were Peregrines, there were nearly always Ravens, but rather more than half the Ravens lacked falcon neighbours." . . ."They were not harmonious neighbours and constant bickering between them was commonplace."

The book's focus is on the ravens of Britain and Ireland. Its foundation is the author's extensive personal experience. Ratcliffe's work with ravens began in 1945 and took him to over 500 nesting places at least once, and a few over 30 different years. Even so, he has drawn heavily on the works of others, citing 295 publications in the bibliography ranging from 1789 to 1996 (with one listed as in press). The result is an information packed synopsis of the current understanding of the biology of the raven.

The Preface (pp. xv–xviii) provides a brief history of raven studies, beginning with William Macgillivray (1837) who was among the first biologists to watch ravens from blinds. It is here that Ratcliffe notes that "The Raven is a bird whose ecology is closely tied up with human affairs and is perhaps more intimately entangled with the cultural life of earlier peoples than any other bird in the whole of history."

The Introduction (pp. 1–6) gives an insight into Ratcliffe's fascination with ravens and how his boyhood explorations of the surrounding hill country in Carlisle grew into a lifelong career of bird study. Chapter 1 (pp. 7–26) charts the raven's course in human history, including a brief section on the prehistoric evidence of ravens in Britain, and longer sections on the raven in myth and legend, and another which follows the raven's transition from scavenger friend in the Middle Ages to

predator foe. In the 1400s and 1500s ravens were widely protected for their services of cleaning filth from towns. Their fall from grace and subsequent persecution began around 1650 and bounties were initiated in many areas by the 1700s. After thousands of ravens were killed for bounties and the effectiveness of shooting and trapping declined, the use of poisons became more popular. Further declines resulted from the increasing popularity of egg-collecting beginning about 1850. In Britain, adequate legal protection did not come until enactment of the Wildlife and Countryside Act in 1981, and in Chapter 12 (Ravens in the Modern Scene) Ratcliffe provides evidence that even today the raven's recovery on the British grouse-moors appears to be held back by continued persecution from modern gamekeepers. The meat of this book fills chapters 2 through 12 (214 pages) which covers the raven's distribution and abundance (Chapter 3), foods and feeding habits (Chapter 4), social behavior (Chapter 5), movements (Chapter 6), associations with other animal species (Chapter 7), breeding biology (Chapters 8–10), territorialism and population regulation (Chapter 11), and how they fit into the modern scene (Chapter 12).

Initially I feared that, with his specific focus on Britain and Ireland, the ravens described by Ratcliffe might have little in common with the ones I have come to know in North America. Indeed, this book focuses a good deal of attention on habitats unfamiliar to me such as sheepwalks of the hill country and grouse-moors of Britain's eastern uplands. In particular, the association of sheep and ravens is an important one in the hills of Britain and Ireland with sheep's wool from carrion featured in 90% of the raven's food pellets in one study. Besides the standard sources of sheep carrion from stillborn lambs (some lamb predation), expelled afterbirths, and expected incidental adult mortality, Ratcliffe describes sheep that die from being "cast" or "couped" (rolled on their backs and unable to right themselves—p. 85), and sheep that die from falling off of ledges on which they were "crag-fast" (having descended partway down a cliff to a grassy ledge from which they could not escape—p. 82). He also describes (p. 72) their ability to follow hunters in apparent anticipation of feeding on the "gralloch" of Red Deer (the discarded entrails). As I read, it was quickly apparent, however, that Ratcliffe's observations and descriptions are quite applicable to ravens of North America and the rest of the Northern Hemisphere. These are the same ravens that I know and their biology and behavior is essentially the same as the ones found throughout at least the northern parts of North America. This feeling was reinforced by 28 pen-and-ink illustrations contributed by Chris Rose. The coastal and mountainous scenery could be Newfoundland/Labrador or Alaska but the essence of the birds captures perfectly the ones I know best in New England. The one constant pattern throughout their range seems to be their ability to successfully exploit the diversity of food resources that are available in each particular area.

In the one short chapter devoted to ravens elsewhere in the world (Chapter 13, 8 pages), Ratcliffe cites the observation of Cramp and Perrins (1994) that the raven "is so wide-ranging that the concept of habitat is hardly applicable. It is one of the most widespread of all bird species in the northern hemisphere . . .". These are birds that can tolerate extreme cold near the Arctic to the desert heat of Death Valley, California, and in the New World range as far south as Nicaragua. In this chapter the ten currently recognized subspecies of Northern Raven are listed and mapped, followed by a brief description of the eight other species of ravens from around the world whose distributions are plotted on the same map (p. 244). This chapter is such a short and cursory treatment that it feels more like an appendix than part of the text. In fact, Appendix 1, which is a systematic listing of the distribution and description of raven flocks and roosts observed in Britain and Ireland, is a page longer.

The final chapter presents evidence, largely in anecdotal form, relating to the reported intelligence of ravens. This is followed by 4 appendices presenting information documenting raven flocks and roosts (appendix 1, 9 pages), describing the varied calls of the raven (appendix 2, 3 pages), detailing the physical appearance of the raven (appendix 3, 3 pages), and listing the scientific names of the 133 animal and 49 plant species referenced in the text (appendix 4, 3 pages). The 27 tables (33

pages) are packed with data on nest site selection, band recoveries, pesticide levels, brood sizes, and related information. Much of this may be of little direct use to readers from outside of Britain and Ireland, but it is consistent with Ratcliffe's apparent desire to present all that he has learned about the ravens of this region, and it provides a very useful point of reference for students of ravens elsewhere in the world.

Ratcliffe has chosen an easy to read, casual style centered around his personal experiences, but he has included numerous citations and lots of data. For me, this was a fun book to read, and I do not expect a more comprehensive book on the Northern Raven anytime soon. It will be my reference of choice for the species.—THOMAS W. FRENCH.

FARMING AND BIRDS IN EUROPE: THE COMMON AGRICULTURAL POLICY AND ITS IMPLICATIONS FOR BIRD CONSERVATION. Edited by Deborah J. Pain and Michael W. Pienkowski. Academic Press, London, England. 1997: 436 pp. $99.95.—The Common Agricultural Policy (CAP) of the subtitle refers to the harmonized agricultural support system of the European Union (EU). The EU is indeed a curious political beast, at least to American eyes: imagine something akin to the progression of the Union as new states joined but compressed in time to about 25 years and with the new partners already well established nations with histories dating to pre-Columban times! The changes and adapting needed would be large indeed, and this is manifest in the environmental policies of the EU. The EU originated in the 1958 European Economic Community (Germany, France, Italy, Belgium, Netherlands, and Luxembourg) but expanded in 1973 to include the United Kingdom, Ireland, and Denmark, later adding Greece in 1981 and Spain and Portugal in 1986 (when the EEC became the European Community). In 1995 when Austria, Sweden and Finland joined what had become the European Union, the largest free trade area in the world had mandatory transnational policies for agricultural and the environment (inter alia), as well as a Birds Directive explicitly for bird conservation.

Farmland covers nearly half of the land surface of the EU and is the major land-use there. Much of the environmental concern arising from agricultural impacts on wildlife derives from the evolution of technological and policy developments that favor intensification and concentration of particular activities: where once a wise farmer managed both stock and small grains, now economics and technology demand specialization on the one or the other. In the UK, where the impetus in this direction began with the 1947 Agricultural Act, long before the CAP was conceived, this intensification is most pronounced, with 16% of all farms above 100 ha (247 acres), 33% of them above 50 ha, and with only 13% smaller than 5 ha. In contrast Greece, a newcomer to the EU, has 78% of its farms this small. One statistic from this book (from a review chapter by Clive Potter) dramatically captures the economic forces toward specialization: a farm family in the Netherlands (intensive highly specialized farming) averages 11 times the income of a Portugese farm family still pursuing environment-friendly mixed farming!

The environmental consequences of systematic financial support for agricultural production have been striking. Fertilizer use in EU countries has increased 400-fold since 1950, machines used increased 45% between 1970 and 1988, and major restructuring—the amalgamation of small farms into fewer large ones—has progressed apace. What has accompanied this intensification of agriculture has been the wholesale removal of hedges, trees, small woods, ponds, and wetlands. Such habitat loss and fragmentation have resulted in the extinction of three species of flowering plant and at least three dragonfly species and one butterfly species in Britain alone. In Germany some 400 species of vascular plants have declined, with 40% of bird species and 50% of mammal species on the "Red List" of threatened and endangered species affected by such intensification. Such data—from a spread of countries across Europe—are the concerns of this book.

The book comprises 14 chapters, with a foreword from the EU Commissioner for Agriculture and Rural Development, Franz Fischler. The first four chapters are introduc-

tory in nature, the first being a scene-setting chapter by the editors and the second (by Clive Potter) an account of changes in farmland in Europe over the last 30 years. The major changes with environmental concern—intensification, specialization, and marginalization—are reviewed as to their origins and propagation within a system of CAP farm support. The chapter by Nigel Robson provides a fascinating historical analysis of the EU's Common Agricultural Policy and the evolution of its relationship to the Directive on the Environment. Robson is a gifted writer with the rare knack of being able to distill a welter of factual material into a coherent synthesis that yet does justice to the intrinsic complexity of the issues. This chapter should be included in the reading lists of every graduate course in resource policy or resource economics. The fourth chapter, by Graham Tucker, describes the importance of farmed landscapes in Europe for bird conservation priorities. Tucker's data synthesis shows that farmland is both the richest habitat for birds of all major European habitats and the one that has the largest proportion of species in trouble across Europe. Within farmland, arable and agriculturally improved grasslands hold the highest number of bird species, including five globally threatened species (Red-breasted Goose *Branta ruficollis,* Imperial Eagle *Aquila heliaca,* Lesser Kestrel *Falco naumanni,* Great Bustard *Otis tarda,* and Corncrake *Crex crex*). Across farmland as a whole, grass conversion, the indirect effects of pesticides, and abandonment of marginal farmland each threaten 30% or more of declining species, and crop improvement impacts another 27% or so. Other major agricultural threats include high stocking rates, drainage, irrigation, and crop specialization. Robson's and Tucker's chapters are probably the most significant in the book for North American readers, not so much for the details—the political and ecological particulars are too different from the U.S. and Canada to be directly applicable—but for the insight they provide into the general issues involved in balancing agricultural land use and bird conservation.

The second part of the book describes issues associated with particular habitats. Three of the chapters are detailed accounts of Spanish issues, covering respectively the ecology of the Spanish dehesas (M. Díaz, P. Campos, and F. J. Pulido), and birds and farming in the pseudosteppes (F. Suárez, M. A. Naveso and E. De Juana). Dehesas are wood pastures or savannahs, typically grazed grasslands populated with holm oak, *Quercus ilex,* or cork oak, *Q. suber,* and provide feeding grounds for such spectacular species as the Spanish Imperial Eagle, Black Vulture, *Aegypius monachus,* and Black Stork, *Ciconia niger.* Pseudosteppes provide a dryland mosaic of habitats of cereal crops, dry legumes, and winter and short rotation fallows that support such rare species as the Great Bustard. Dehesas and pseudosteppes are rather marginal farming systems vulnerable to intensification, yet unprotected as to their conservation value. Similarly, low intensity, extensive grazing systems are economically marginal but have long been of significance for raptors in Spain (Chapter 5, by J. A. Donázar, M. A. Naveso, J. L. Tella, and D. Campión). The short to medium fallow rotations (5–7 years) in steppe areas provide a mosaic of winter stubbles and grassland that supports many small birds that in turn provide food for raptors; and free-ranging livestock, particularly sheep, provide carcasses for vultures. As in all the habitat chapters, the consequences for birds of the current CAP and of possible future changes in it are explicitly reviewed. For these grasslands, for example, favorable headage payments under the CAP have led to sheep being kept on the grasslands for longer, leading to over-grazing and increase in bare ground. In addition, increased use of pesticides on crops is reducing arthropod abundance and the abundance of passerines they once supported.

Chapter 6 is a further contribution by Dick Potts to the bird ecology of cereal ecosystems and continues his unrivaled, now 28-year-old study of the Gray Partridge *Perdix perdix.* He concludes that four elements of cereal intensification—use of herbicides, abandonment of undersowing to establish grass/legume leys, cessation of arable farming in hill regions, and summer use of foliar insecticides—have reduced insect abundance and increased chick starvation, with an 83% reduction in partridge numbers across Europe. His data notably show that even the 1992 reforms of the CAP—intended to ameliorate the environmental damage of production-oriented subsi-

dies while at the same time bringing the runaway financial costs of the CAP under control—have failed to redress the partridge's problems from intensification. Chapter 8 focuses on another cereal system, that of rice cultivation. Here Mauro Fasola and Xavier Ruíz discuss the possible role of rice production as a substitute for wetlands being drained with CAP subsidies. A chapter by Norbert Lefranc analyzes how intensification has induced landscape-level changes that appear to account for the precipitous decline of most shrike (*Lanius* sp.) populations in western Europe. The remaining two habitat chapters comprise another contribution by Albert Beintema to the ecology of grassland birds (here with coauthors Euan Dunn and David Stroud), and a chapter by Andy Evans reviewing the ecology of seed-eating species on mixed farmland in the United Kingdom. Evans shows that the loss of mixed farming may have been responsible for the major declines in populations of seed-eating birds in the UK: eight of these species have declined by 52–89% since the late 1960s. The editors provide a synthesis chapter, largely recapitulating the recurrent themes of the individual chapters. Here American proponents of the Farm Conservation Reserve Program will note the conclusion that set-aside (the EU's equivalent of the CRP) has substantial conservation potential that is being realized for some but not all species. The final chapter is a closing review by James Dixon on the future threats and opportunities of European agriculture. This chapter is less a review than a futurist's view of the CAP but at its core is the idea that agricultural policy must eventually turn from an emphasis on production to an emphasis on, and re-distribution of the benefits of the policy towards social and environmental purposes.

The scope of this book is more accurately captured by its subtitle than by its title and it is only the handful of ecological chapters that match expectations raised by the title. Only 6 of the European Union member nations are represented among the 23 authors, and 19 of these are from just 2 countries (Spain 10, United Kingdom 9). Five of the authors are from the same organization (the UK's Royal Society for the Protection of Birds), testament to the strength of the research and lobbying effort sustained financially and organizationally by the RSPB but not conducive to much diversity of views of the problem. (The book was in fact published for the RSPB by Academic Press). The narrow national base of authorship left me feeling dissatisfied with the book's lop-sided geographical coverage, with Spain, in particular, receiving disproportionate treatment for a European book. Although the bias is offset in part by the excellent review articles already mentioned, one wishes for contributions reflecting some of the fine land-use and farmland ecology studies performed in Sweden, Denmark, and Germany. The lack of a biogeographic perspective is also noticeably missing (though Potter does note the regional geography of farming in his review).

Traditional low intensity farmed landscapes have long been harbors of rich biodiversity, yet agricultural change is now the most frequent cause of European bird population declines. Graham Tucker's conclusion is striking: "... farmland bird habitats are now, quite simply, the foremost bird conservation priority in Europe." Why have traditional conservation measures failed European birds so badly? The problem is that conservation interest has focused essentially only on site-based measures such as designation of protected areas and the establishment of nature reserves. These fail for agricultural birds for three main reasons. First, most such species are widely dispersed in one or more stages of their annual cycle. Second, emphasis has been on protecting natural habitats, in part the result of the mistaken belief that agricultural habitats are of low conservation importance. Third, and in my view perhaps the most important, statutory protection of sites does not provide for the maintenance of the traditional, often low intensity, farming systems that many of the most important bird species depend on. Despite current emphasis on landscape approaches to conservation, this point is perhaps the one least developed in our present thinking about conservation biology on this side of the Atlantic. This book is a salutory reminder of the need to broaden our horizons if grassland and farmland birds are to receive effective conservation support.—RAYMOND J. O'CONNOR.

THE BIRDS OF THE CAPE VERDE ISLANDS: AN ANNOTATED CHECK-LIST. By Cornelis J. Hazevoet. B.O.U. Check-list No. 13.British Ornithologists' Union, Tring, Herts, UK. 1995: 192 pp. £ 17.00 cloth (ca. US$ 26.00).—For anyone even remotely interested in distributional ornithology, the B.O.U. Check-lists are goldmines of information attractively presented, reasonably priced, and usually standards against which many avifaunal efforts can be measured. That for the Cape Verde Islands (hereafter, CVI) is no exception.

Following the Check-lists' recent trend of using a cover color photo of a bird typifying the area (in this case, a splendid Brown Booby in flight), after the usual front matter the book is divided into three major sections. First is the Introduction (pp. 15–80), covering history; geology and geography; climate; vegetation and habitat; breeding seasons; migration; conservation; zoogeography; endemics; and the history of CVI ornithological exploration. Eleven excellent black-and-white, geopolitical maps depict the ten main islands but none of the (unnumbered) islets. Second, and the heart of the book, is the Systematic List (pp. 81–147), treating 144 numbered "species" (see below why I put this term in quotes).

A 48-figure, 24-page, color section features habitats in the CVI and stunning photos of such birds as Cape Verde (CV) Cane Warbler, CV Swift, CV Little Shearwater, CV Kite, CV Shearwater, the whimsically translated Neglected Kestrel, Brown-necked Raven, Raso [sic] Lark, Iago Sparrow, and Hoopoe Lark. The Frontispiece was a letdown: a black-and-white photo of the nest and plain white egg of Fea's Petrel, even though probably the first ever published.

Several of the extremely useful Appendices (pp. 148–167) that have become hallmarks of B.O.U. Check-lists follow: omitted species; taxa named from CVI specimens; banded (ringed) birds recovered in the CVI; a table of CVI ornithological explorations (encapsulating information presented in the Introduction); a gazetteer with full latilong data; local names of CVI birds; and the inter-island distribution of CVI breeding species. A bibliography (pp. 168–174) closes the book.

What quickly sets this volume apart from other B.O.U. Checklists is Appendix 4 (pp. 153–157), "Species concepts and systematics." This somewhat surprising section is an unabashed *apologia* for the Phylogenetic Species Concept (PSC), of which Hazevoet is a principal protagonist. My first reaction was that its use was inappropriate in a faunal monograph. Subsequently, I concluded that he has perfect right to do so, even if I might not agree with it. Moreover, it is one of the best—if not the best—concise expositions of the PSC that I have read.

The upshot is that several CVI taxa that the Biological Species Concept (BSC) might consider allopatric races, Hazevoet treats as separate species and therefore CVI endemics. He splits them into 11 'landbirds' [*Ardea* (*purpurea*) *bournei, Milvus* (*milvus*) *fasciicauda, Buteo* (*buteo*) *bannermanni, Falco* (*tinnunculus*) *neglectus, F.* (*tinnunculus*) *alexandri, F.* (*peregrinus*) *madens, Apus* (*unicolor*) *alexandri, Tyto* (*alba*) *detorta, Alauda razae, Acrocephalus* (*rufescens*) *brevipennis,* and *Passer* (*motitensis*) *iagoensis*] and 3 seabirds [*Pterodroma feae, Calonectris,* (*diomedea*) *edwardsi,* and *Puffinus* (*assimilis*) *boydi*]. Readers will note that a number of these are also widely regarded as distinct species under the BSC (e.g., Fea's Petrel, Raso Lark, and Iago Sparrow).

He sinks as not "diagnosably distinct" two seabird subspecies (*Pelagodroma marina eadesi* and *Fregata magnificens lowei*) and eight landbird races (*Coturnix c. inopinata, Cursorius cursor exsul, Halcyon leucocephala acteon, Eremopteryx n. nigriceps, Ammomanes c. cincturus, Alaemon alaudipes boavistae, Sylvia conspicillata orbitalis,* and *Sylvia atricapilla gularis*), considering them either ends of clines or only weakly morphologically differentiated. Neither is he keen on the very concept of subspecies ("It will, therefore, probably be better to abandon the 'subspecies' category altogether and look for other ways of describing intraspecific variation"), although he finds 'subspecies' (always pejoratively in quotes) useful, as do many of us, in deducing the origins of migrants and vagrants (in the present volume: Little Bittern, Black-crowned Night Heron, Intermediate Egret, Eurasian Spoonbill, Eurasian Teal, Eurasian Kestrel, Collared Pratincole, Little Ringed Plover, Dunlin, et mult. al.).

The species accounts are informative and up to date, usually with such subheadings as

movements, breeding, taxonomy, and where appropriate, status broken down island by island. English names regrettably fail to meet a globally-unique standard, perpetuating such quintessentially Anglocentric names as "Night Heron," "Storm Petrel," "Gannet," "Teal," "Pochard," "Coot" and of course that old favorite, "Swallow"—a bit disappointing in a B.O.U. publication.

A close reading of the entire book was rewarding, and, amazingly, I noticed only a single (trivial) typo. I was disappointed that no measurements were given in discussions of any of his taxonomic diagnoses, and I would have preferred more detailed treatment of geostrophic and seasonal wind patterns, and of water temperatures and currents. Regrettably, there were neither bathymetric nor vegetative cover maps, both of which would have aided readers in interpreting distribution and abundance patterns.

Under each species account it would have made far better zoogeographic sense, especially to readers unfamiliar with the global ranges of treated species, to have had capsule descriptions of their complete ranges before details of their CVI distributions. Likewise, the useful term "vagrant" is probably debased when applied to species whose occurrence in a given area may merely be a function of numbers of observers and time afield—and not of true geographical vagrancy. For example, I suspect that in the CVI, Sooty Shearwater, Red-footed Booby, Black-crowned Night Heron, and Little Bittern, to name a few, fall into the former, not the true vagrant, category. "Expected but infrequently recorded" would be a more accurate (but longer) term.

One feature I applaud is the inclusion in the appropriate systematic locations of bracketed species that have occurred within the CVI area but only at sea, or which have never been found anywhere in the area but ought to occur. I might make the case for highlighting these in a collected Appendix rather than burying them in the text body, but either way it's useful information.

The CVI sit at sea some 300 miles (500 km) west of the bulge of West Africa, where many hurricanes form in September in the intertropical convergence zone, routinely reaching the Lesser Antilles [ca 1800 miles (2900 km) west] and occasionally even the continental U.S. Thus, species present as migrants or vagrants in the CVI also need to be considered candidates for Western Hemisphere occurrence. In this regard, it is fascinating and occasionally eye-opening to consider the occurrence, frequency, and subspecific identity of the species in the CVI.

This is a splendid volume, chock full of information, beautifully presented, well-bound (it lies flat), and these days, a bargain at £17.00. I recommend it enthusiastically.—P. A. BUCKLEY.

THE BIRDS OF AFRICA, volume 5 [BOA5]. Edited by Emil K. Urban, C. Hilary Fry, and Stuart Keith. Academic Press, London. 1997: xix and 669 pp., 32 color plates, numerous line drawings and maps. $149.00 (cloth).—This series, with its well-researched species accounts and with all species and distinctive subspecies illustrated, has become the standard work on African birds. In this volume, the authors of the species accounts are C. Erard, C. H. Fry, L. G. Grimes, M. P. S. Irwin, S. Keith, P. C. Lack, R. de Naurois, D. Pearson, A. Prigogine, A. Tye, and E. K. Urban; the color plates are by Martin Woodcock, and the line drawings of birds and nests are by Ian Willis.

The main text of BOA5 is 600 pages of species accounts for Turdidae thrushes (*Monticola, Zoothera,* and *Turdus*; the others were in BOA4), Sylviidae Old World warblers, Muscicapidae flycatchers, Monarchidae paradise flycatchers and monarchs, and Platysteiridae wattle-eyes and batises. Measurements of wing, tail, bill, and tarsus and body weights are reported by sex. Subspecies are compared and sometimes characterized by measurements. Maps show species distributions. Other material includes regional locality maps, family and genus descriptions, a list of song disks and cassettes and names of recordists as compiled by C. Chappuis, notes to correct previous volumes, lists of full References by region and by taxonomic group, and an index with scientific (genus, species, subspecies) and English species names.

The species accounts are generally accurate and informative, though some are long on de-

scription, feather by feather, and frugal on documentation in spite of the extensive References lists. BOA5 has 0–5 (to 11) references at the end of each species account and the text usually cites a few others. There has been so little fieldwork on many African songbirds that it is worth documenting what is known with more text citations. Why not include the sources of statements that many warblers are parasitized by *Prodotiscus* honey-guides, and certain warblers are parasitized by all three families of African brood parasites (cuckoos, honey-guides, and the Viduidae Cuckoo-finches)? In error, Winding Cisticola (*C. galactotes*), Pectoral-patch Cisticola (*C. brunnescens*), and Singing Cisticola (*C. cantans*) are said to be parasitized by Pin-tailed Whydahs (*Vidua macroura*). The error traces to breeding records in Ethiopia (R. E. Cheesman and W. L. Sclater, 1935. Ibis 13:594–622; 1936. 14:163–197) where the young brood parasites were originally identified as whydahs, but in fact were Cuckoo-finches (*Anomalospiza imberbis*), as reidentified in Cheesman's specimens in the Museum of Natural History at Tring and recognized by J. P. Chapin (1954 Bull. Amer. Mus. Nat. Hist. Bull. 75B) and H. Friedmann (1960 U. S. National Museum Bull. 223).

The decisions about species limits and subspecies include enough calls of judgment to keep field workers busy, and for others interested in biological species. BOA5 will be a useful baseline for fieldwork in recording songs and working out details of nesting and breeding behavior. To illustrate, one question involves Winding Cisticola or Black-backed Cisticola (*Cisticola galactotes*)—the two English names are appropriate as more than one species is probably involved. Calls and songs vary geographically, but no vocalizations in south-central Africa correspond with the watch-winding call in West Africa that gives the name "Winding Cisticola." In northwestern Zimbabwe on the upper Zambezi River the local "Black-backed Cisticola" have never been heard with a winding call like those of West African birds, and the local "*C. galactotes*" in my photos look like *luapula* in northeastern Zambia. Also, in northwestern Zimbabwe a song ("dzitdzidzee") more like the winding call of West African *C. galactotes* is given by Chirping Cisticola *C. pipiens* in reedbeds alongside *C. (galactotes) luapula*. The case illustrates the need for more fieldwork and underscores the importance of BOA5 as a basis from which to expand our current information.

The BOA notes on song lead one to appreciate the conditions in which songs are criteria of species identity. Some forms of Bar-throated Apalis (*A. thoracica*) do not respond to each other's songs on playback, and several species may be involved. Songs also differ between distinctive geographic color forms of Yellow-breasted Apalis (*A. flavida*) and these may include more than one species. In contrast, Black-headed Apalis (*A. melanocephala*) songs vary geographically independently of the variation in plumage. Another complication in using song behavior as a species criterion is that two species (*A. alticola*) and Chapin's Apalis (*A. chapini*) may countersing with each other. On the other hand, the songs of some clearly divergent thrush species are similar or indistinguishable. Among the results that encourage us to record all these African songbirds wherever we find them, African Thrush (*Turdus pelios*) and Olive Thrush (*T. olivaceus*) differ in song, mostly phrases of 2 notes in *T. pelios* and 5–8 notes with alternating high and low notes followed by soft phrases in *T. olivaceus*. This helps clear up earlier reports of the species in the wrong areas.

BOA life history data will be of interest to tropical ecologists and behavioral biologists. In addition, the text can help guide systematic ornithologists. One bird of systematic interest is Oriole Warbler or Moho (*Hypergerus atriceps*); its plumage suggests an Asian bulbul, while the nest is like a sunbird or an East African Grey-capped Warbler (*Eminia lepida*), and a French name (not in BOA5) is Timalie à tête noire, indicating a babbler. Another theme involves the relationships and dispersal history of warblers in Africa and Asia. A possible Asian connection involves two "African tailorbirds" *Artisornis*, where one species is sometimes placed in *Apalis* and the other in *Prinia* (both have 10 rectrices). The two might be related to the Asian tailorbirds (*Orthotomus*), though other African warblers build tailorbird-like nests with the leaves stitched together: *Camaroptera* and some *Cisticola* also do this. *Prinia* may be paraphyletic in Africa

with more than one dispersal from Asia where other prinias occur. BOA5 comments give us a reality check on the geographic scale that is appropriate in avian systematics.

The Birds of Africa series continues to improve with information on natural history and systematic summaries, clear maps, and useful and attractive color plates. This volume brings together what is known for each species and points out where good field observations are needed. Everyone with an interest in African birds should have the series, or make it available in their institutional library.—ROBERT B. PAYNE.

WARBLERS OF EUROPE, ASIA AND NORTH AFRICA. By Kevin Baker. Princeton Univ. Press, Princeton, New Jersey. 1997: 400 pp., 48 color plates, 145 range maps, many black-and-white sketches. $49.50.—The latest volume in the "Helm" series of family monographs covers a portion of the traditional subfamily Sylviinae. The geographical range is of the whole Palearctic, North Africa, and the rest of mainland Asia. One hundred forty five of the approximate 350+ species in the subfamily are treated.

The format of this series is now well known. A brief introduction is followed by the 48 colored plates accompanied by a small range map for each species. The main text treats the species accounts under the headings: Identification, Description, Geographical Variation, Moult, Voice, Habitat and Behaviour, Distribution, Measurements, and References. Individual accounts may be 3–4 pages long.

The birds of this subfamily present some of the most difficult identification problems in ornithology. Some genera consist of a series of L.B.J.s (Little Brown Jobs). The genus *Phylloscopus* is represented by 37 species, all of which will look like fall immature Pine Warblers (*Dendroica pinus*) to most readers of the Bulletin. The omission of sub-Saharan Africa means that only two species of the really difficult genus *Cisticola* are included and we are saved from having to face the 43 African species with their participial English names.

The text contains less information about the habitat and behavior of the birds than some of the other books in the series and is concentrated on identification and description. For a species picked at random, Greenish Warbler (*Phylloscopus trochiloides*), 30.5 column-inches are devoted to identification and Habitat and Behaviour are covered in 4 column-inches. In many cases the extensive identification space is devoted to comparing "Confusion Species," a real plus in these difficult genera. Identification by song is important in this group, but the Voice section of the text is not very helpful.

The author-artist has been quite successful with his color plates which are the best I have seen in this series of books. The figures of the few members of the genus *Sylvia* with which I have had experience and those whose museum specimens I examined all seemed to be accurate portrayals. The color reproduction may be a little too bright but the shapes and poses of the birds are good.

The range maps are somewhat better than in most of this series. They are still too small, but the shade of yellow makes better contrast with the white page and the base maps have enough detail to identify the area. Unfortunately in a few cases the base map did not print and the maps consist of a blue blob (winter range) and a yellow blob (breeding range) hanging in space.

As has been mentioned in reviews of other books in this series (c.f., Wilson Bull. 109: 366–367, 1977) it is unlikely that anyone would carry this on a trip abroad and since only one species, the Arctic Warbler (*Phylloscopus borealis*) occurs in North America (only western Alaska) the main reason for buying this book is to expand one's bookshelf devoted to Birds of the World. For that purpose this is a fine addition.—GEORGE A. HALL.

DEMOGRAPHY OF THE NORTHERN SPOTTED OWL. Edited by Forsman, E. D., S. DeStefano, M. G. Raphael, and R. J. Gutierrez. 1996. Studies in Avian Biology 17:1–122. $20.00 (available from Cooper Ornithological Society, % Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, California 93010.—The Northern Spotted Owl (*Strix occidentalis caurina*) is perhaps the best known symbol of problems

and conflict resulting from the effects of exploitation of natural resources on endangered species. This old growth species from the Pacific Northwest has been both the instrument used to draw attention to the disappearance of old growth forests and the instrument used to attack the Endangered Species Act. In recent years the battle has become more refined such that, as Gutierrez et al. note in their chapter on the history of demographic studies of this bird, "demographic information and population models have become 'weapons of choice' among competing advocacy groups."

The controversies surrounding Spotted Owls and old growth revealed a serious lack of data on the population dynamics of the species, thus stimulating several mark-recapture studies during 1985–1990. This volume includes papers presented at a 1993 workshop held in Fort Collins, Colorado, with additional papers added on background and techniques and synthesis of results to create a more complete publication. The individual papers are presented in journal format, with a single literature cited section at the end. An appendix defines symbols and technical terms used. Studies included in this volume encompass the work of agency and university biologists, with the notable withdrawal of data from three forest industry studies. Data from 11 studies (1 in northern California, 2 in Washington, and 8 in Oregon) are included, all of which were collected using similar protocols that are discussed in the chapter by A. B. Franklin et al. Thus it is argued that the resulting data can be compared and combined. The combined effort in these studies resulted in 6059 owls banded, a sample size rivaling those enjoyed by those studying some songbirds. These resulted in over 6500 captures/recaptures of birds initially captured as territorial adults. Thus, sample sizes were large enough to allow demographic inferences from capture-recapture analyses.

From analyses of these combined data sets, K. P. Burnham et al. conclude that (1) annual survival of females captured as adults has declined significantly over time and that a similar trend for males is suggested, the population of resident females is declining on most of the 11 areas, and the rate of population decline is accelerating. Raphael et al., in the final chapter, suggest that these declines are a result of "extensive loss and fragmentation of an estimated 80% of late-seral stage forest within the last 40 years."

There's a lot of conservation history within these pages, a lot of evidence of the contentious nature of recent Spotted Owl history, and it seems in reading this volume that considerable thought went into every word. It seems as if every step of the studies—from field work to analyses to interpretation—was in need of justification and subjected to incredible scrutiny. It's as if the words might end up in court. And well they might.—JEROME A. JACKSON.

SHRIKES, A GUIDE TO THE SHRIKES OF THE WORLD. By Norbert Lefranc, illus. by Tim Worfolk. Yale University Press, New Haven, Connecticut. 1997: 192 pp., 16 color plates with caption figs., 33 range maps, more than 20 unnumbered text figures. $35.00 (cloth).—The Laniidae are the only passerine family that is strongly adapted for predation. Most members of this unique family impale or wedge prey. This potentially serves two functions: one is to form a storage site, or "larder" where food can be stockpiled; the other is to anchor down prey items too big to swallow whole, such that smaller pieces can be pulled off and eaten.

This book is a thorough treatment of our current knowledge about this fascinating family. It begins with an excellent overview of the taxonomy of this group. Until quite recently, as many as 74 species were placed in this family, including bush-shrikes, tchagras, gonoleks and helmet-shrikes. This initial section gives a superb account of the history and logic behind narrowing down the family to 30 species in just three genera: 26 species of *Lanius*; two of *Corvinella*, and two of *Eurocephalus*. It also provides extremely helpful discussions of species problems within the genus *Lanius*.

Following the taxonomic considerations is a well-written, detailed, and useful overview of the biology (ecology, behavior, conservation biology) of each of the family's three genera. Oddly, on page 41, after the end of these two introductory chapters, there suddenly appears a section entitled "Style and Layout of

the Book". One wonders why it is located part way through the book, instead of at the beginning where it seems to belong.

Following these introductory sections are the individual species accounts. The coverage is broad and careful; where information is lacking, this is pointed out. The material is up-to-date, and there is an impressive bibliography of more than 600 references. Given all this, I was surprised to find the claim that it is impossible to tell male from female Loggerhead Shrikes based on plumage. At least in the population I worked on in central Washington State, adult males were consistently bluer gray, with females being somewhat browner in color. However, this is a minor quibble. Overall the species accounts are a superb resource, presenting well-organized information on behavior, ecology, migration patterns, and conservation biology of every shrike species.

One of the real strengths of the book is the set of 16 color plates by Tim Worfolk. These outstanding plates depict 140 individuals, and include adult males, adult females, and juveniles of all 30 species, as well as many distinct races and even a few hybrids. In addition, among the many line drawings are half a dozen detailed diagrams of wings and/or tails showing subtle interspecific differences between species (for birds in the hand).

Typographical errors were remarkably few and of the modern kind, i.e., those that pass through spell-checks. Thus one finds a redundant "closely" (p. 29); on instead of in (p. 103); nest cap for nest cup (p. 115); and the like. The most serious of these was "invertebrates" where clearly what was meant was vertebrates (page 15).

A very nice feature is a list of "Useful Addresses" where anyone newly infected with the "shrike virus" can write to contact others similarly infected, although it is perhaps a bit surprising that no email addresses are included in this list.

This delightful book represents a solid contribution to our understanding of the biology and problems of conservation of this fascinating family. I recommend this beautifully illustrated and informative book to anyone interested in shrikes, or indeed anyone who enjoys well-written accounts of avian natural history.—SUSAN M. SMITH.

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MIGRATION OF WESTERN SANDPIPERS: LINKS BETWEEN THEIR ALASKAN STOPOVER AREAS AND BREEDING GROUNDS

MARY ANNE BISHOP[1,4] AND NILS WARNOCK[2,3]

ABSTRACT.—Thirty-two radiomarked Western Sandpipers (*Calidris mauri*), tagged in California and Washington, were relocated at stopover and breeding sites north and west of the Copper River Delta, Alaska. At Cook Inlet, Alaska, seven of the nine relocated birds were at Redoubt and Kachemak bays. Only 1 of the 17 birds relocated on the Yukon-Kuskokwim Delta had been previously detected at Cook Inlet. Detections of birds in western Alaska provide evidence that the Yukon-Kuskokwim Delta is the final breeding destination for many of the birds migrating through San Francisco and other Pacific Coast areas. The Mulchatna River area, 325 km southeast of the Yukon-Kuskokwim Delta, may support a breeding population of Western Sandpipers. *Received 12 Jan. 1998, accepted 30 July 1998.*

The Western Sandpiper (*Calidris mauri*) has been the subject of much recent research (Warnock and Takekawa 1995, 1996; Butler et al. 1996; Iverson et al. 1996). As with most Arctic breeding shorebirds that migrate through North America, much remains to be learned about their use of different areas during various stages of the annual cycle. In Alaska, Western Sandpipers breed primarily on the Alaska Peninsula north of the Aleutian Range to Nelson Lagoon (Gill et al. 1981; Kessel and Gibson, pers. comm.), along the western and northern coasts from Bristol Bay and the Kashunuk River to the Seward Peninsula, and less frequently to Point Barrow and northeastern Siberia (American Ornithologists' Union 1983). They winter along both coasts of North America, from southern Washington and southern New Jersey south through Central America to Peru (Wilson 1994).

Work we have done with others (Iverson et al. 1996) showed that Western Sandpipers radiomarked at San Francisco Bay in April rapidly migrate north towards Grays Harbor and the Fraser River Delta and then northwest towards their breeding grounds, with stops at major estuaries along the coast. We tracked five birds as far northwest as Cook Inlet, Alaska, approximately 350 km west of the Copper River Delta, a key spring stopover area (Isleib 1979, Iverson et al. 1996). It has been speculated that Cook Inlet is the next important stopover site for Western Sandpipers migrating from the Copper River Delta (Isleib 1979, Senner 1979, Senner et al. 1981), but information remains scarce on spring migratory routes farther west. In this paper, we report on the migration of radiomarked Western Sandpipers captured in California and Washington to areas west of the Copper River Delta and their relative use of sites intermediate between

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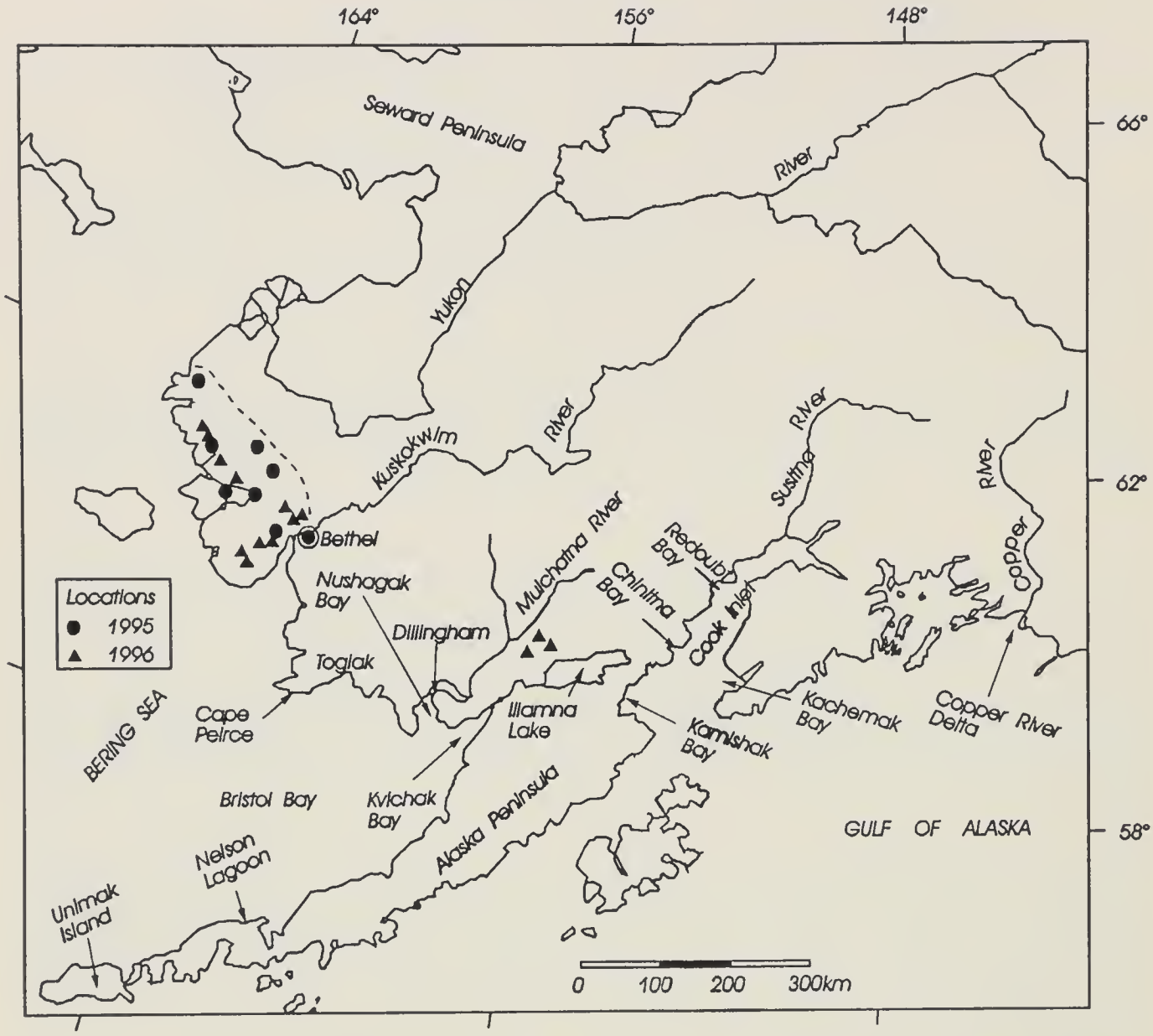

FIG. 1. Alaska monitoring sites west of the Copper River Delta and relocations of radiotagged Western Sandpipers on known and probable breeding grounds. Dashed line denotes eastern extent of Yukon-Kuskokwim Delta survey area.

the Copper River Delta and the Yukon-Kuskokwim Delta.

METHODS

We captured Western Sandpipers between 17–30 April 1995 (n = 61) and 17 April–3 May 1996 (n = 71) at San Francisco Bay, California; Grays Harbor, Washington; and Honey Lake, California (a western Great Basin wetland). Birds were trapped and radiomarked using methods described by Warnock and Warnock (1993) and Warnock and Bishop (1998). Sex was determined based on exposed culmen measurements (males < 24.2 mm, females > 24.8 mm; Page and Fearis 1971). Radiotransmitters were active up to 42 days and had a retention time of at least seven weeks (Warnock and Warnock 1993). Detection of radio signals varied by method: range was less than 2 km from the ground using a hand-held antenna and 4–10 km from an airplane.

Cooperators communicated daily about departures and arrivals of radiomarked birds at each site. We searched for radiomarked sandpipers from fixed-wing aircraft at five areas west of the Copper River Delta, Alaska: Cook Inlet, Lake Iliamna to Mulchatna River (1996 only), Bristol Bay, Alaska Peninsula, and Yukon-Kuskokwim (YK) Delta (Fig. 1). Aerial flights varied in number and timing by area and year (Table 1), and were conducted 150–1200 m above ground level depending on the area and weather. Yagi or H antennas were fixed to each wing strut of the aircraft. During 1996, additional monitoring was conducted from the ground at Cape Peirce and Susitna Flats.

Three cooperators regularly monitored intertidal areas at Cook Inlet from Chinitna Bay north to Susitna Flats on the west side of the inlet, and at Kachemak Bay/Fox River Flats area (hereafter referred to as Kachemak Bay) on the east side of the inlet. Intertidal areas at Bristol Bay were monitored regularly at Cape

TABLE 1. Telemetry methods (A = aerial, G = ground) and field effort (days) for monitoring migratory movements of radiomarked Western Sandpipers west of the Copper River Delta, Alaska, April–May 1995, 1996.

Location	Method	Monitoring dates 1995	Monitoring dates 1996
Cook Inlet			
Susitna Flats-N. Redoubt Bay	G		24–25 April, 8–15 May[c]
	A	2, 4, 6, 8, 10, 12, 13, 16, 18 May	
Redoubt-Chinitna Bays	A, G	3–5, 8–10, 12, 14 May[a]	1, 3, 6–11, 13, 14 May[d]
Kachemak Bay/Fox River Flat	A	29 April–16 May[b]	28 April–17 May[e]
Lake Iliamna-Mulchatna River	A		29, 31 May
Bristol Bay			
Kvichak-Nushagak Bays	A	2, 3, 5, 11, 15, 16 May	28 April–22 May, 5 June[f]
Unimak-Nelson Lagoon, Alaska Peninsula	A	11, 17, 18 May	7, 10, 14, 15, 17, 20, 29, 31 May, 1 June[g]
Dillingham-Togiak	A		30 April, 17, 20, 21 May
Cape Peirce, Hagemeister St.,	G		3–28 May
Yukon-Kuskokwim Delta	A	13, 22, 23 May	8, 10, 13, 16, 20, 23 May

[a] 1995: Flight 12 May, Redoubt Bay to Iliamna Bay; flight 14 May, Redoubt Bay to Cape Douglas.
[b] 1995: No flights 30 April, 5, 6 May.
[c] 1996: Ground effort at Susitna River.
[d] 1996: Redoubt Bay to Augustine Island 7–8 May only; other flights Chinitna Bay to West Foreland (N. Redoubt Bay).
[e] 1996: No flight at Kachemak Bay 30 April, 1, 12 May.
[f] 1996: No flights 5, 6, 12, 13, 16, 20 May. Most flights Egegik to Cape Constantine. Flight 9 May included Kulukak Bay. Flight 5 June inland from Naknek to Kulukak Bay.
[g] 1996: West side of Alaska Peninsula. Flights varied, Unimak (east) to Moffet Bay, and Cold Bay to Nelson Lagoon. 7 May flight followed coastline.

Peirce (westernmost Bristol Bay, 1996 ground coverage only), and Nushagak and Kvichak bays. On the Alaska Peninsula between Unimak and Nelson Lagoon, lowland areas within 32 km of the coast were monitored for radiomarked sandpipers concurrent with low-level aerial surveys for other wildlife species (Table 1). Upland areas were also monitored opportunistically on four flights between Togiak and Dillingham. Potential breeding habitat was surveyed for radioed birds twice between Lake Iliamna and Mulchatna and once at Bristol Bay. On the YK Delta, regular monitoring flights for breeding birds alternated between upland areas northwest and southwest of Bethel.

For analyses, dates were converted into Julian dates (JD). Statistical analyses were performed using STATA (ver. 5.0, StataCorp, College Station, TX 1997). Significance level for tests was $P \leq 0.05$. Data are reported as $\bar{x} \pm 1$ SD.

RESULTS

Of 132 Western Sandpipers radiomarked in California and Washington, we detected 32 at monitoring sites north and west of the Copper River Delta: 14 in 1995 and 18 in 1996 (Table 2). In 1996, one bird was detected at two locations, first in the western Cook Inlet and 12 days later on the YK Delta. Earliest date for monitoring was 28 April (Kachemak Bay,

TABLE 2. Detections of radiomarked Western Sandpipers at areas north and west of the Copper River Delta, Alaska. May 1995, 1996.

		No. banded[a]		Cook Inlet		Bristol Bay		Mulchatna[b]	Yukon-Kuskokwim Delta	
Banding location	Sex	1995	1996	1995	1996	1995	1996	1996	1995	1996
San Francisco	Male	16	11	0	0	0	2	1	2	0
	Female	13	15	3	3	1	0	1	1	3
Honey Lake	Male	12	7	0	0	0	0	0	0	0
	Female	6	5	0	0	0	0	1	1	0
Grays Harbor	Male	7	21	1	1	1	0	0	1	6
	Female	7	6	1	0	0	0	0	2	0
	Unknown	0	1	—	0	—	0	0	—	1

[a] Does not include banded birds that lost radios, had interference with other radios in the Bristol Bay area or were known to be predated.
[b] Not monitored in 1995.

1996) and the first bird was detected on 2 May (1995) at Kachemak Bay.

Nine radiomarked birds were detected at four sites in Cook Inlet, including four at Redoubt Bay, three at the Kachemak Bay, and one each at Tuxedni and Chinitna Bays (western Cook Inlet). Six of the nine birds (66%) had previously stopped on the Copper River Delta, including one bird that returned to the Copper River after a one day stay at Kachemak Bay. Arrival dates at Cook Inlet ranged from 2–14 May ($\bar{x}$ = 9 May ± 4 days, n = 9). We failed to find a significant difference between arrival date of San Francisco birds and Grays Harbor birds (Kruskal-Wallis: χ^2_1 = 2.40, $P > 0.05$), but the power of this test is low (Table 2).

Four radiomarked birds were detected in northeast Bristol Bay: three at Kvichak Bay and one on the Igushik River near Nushagak Bay. Two of the four birds had stopped at the Copper River Delta. The other two birds had been previously detected only at their San Francisco and Grays Harbor banding sites. Arrival dates at Bristol Bay ranged from 3–11 May ($\bar{x}$ = 8 May ± 4 days, n = 4). No radiomarked birds were detected on survey flights along the Alaska Peninsula, at the Cape Peirce ground monitoring site, nor on flights between Dillingham and Togiak.

Combining years, 20 birds were relocated on known or suspected breeding grounds (Table 2, Fig. 1). One male and two females were located between the Stuyahok and Koktuli rivers northeast of the confluence of the Nushagak and Mulchatna rivers on 29 and 31 May 1996. All three birds had previously stopped at the Copper River Delta. On the YK Delta, 17 birds were detected at locations up to 120 km from the coast. Ten of the 17 birds are known to have stopped on the Copper River. Two birds, both banded at Grays Harbor, were not detected at any monitoring site except the YK Delta.

Although ground crews at the YK Delta first recorded Western Sandpipers on 8 May in 1995 and 7 May in 1996 (Ely, pers. comm.), first date of detection for the 17 radiomarked Western Sandpipers at the YK Delta was 13–23 May ($\bar{x}$ = 20 May ± 4 days, n = 17). We found no significant difference in first date of detection at the YK Delta for birds radiomarked at San Francisco (n = 6) and birds radiomarked at Grays Harbor (n = 10, Kruskal-Wallis: χ^2_1 = 3.40, $P > 0.05$; insufficient data to test Honey Lake birds). We also failed to find a significant difference in the number of Honey Lake birds (1 of 30) and the number of San Francisco birds (6 of 55) detected at the YK Delta (χ^2_1 = 1.47, $P > 0.05$), and in number of Grays Harbor (10 of 42) vs San Francisco birds detected at the YK Delta (χ^2_1 = 2.9, $P > 0.05$). Grays Harbor birds were significantly more likely to be detected at the YK Delta than Honey Lake birds (χ^2_1 = 5.7, P = 0.02).

DISCUSSION

Isleib (1979) suggested that after the Copper River Delta, lower Cook Inlet (Kachemak and Kamishak Bays; Fig. 1) provided the next suitable stopover habitat for Western Sandpipers migrating toward their breeding grounds. Kamishak Bay has rarely been monitored because of its remote location (only one survey during this study) whereas historically as many as 100,000 small sandpipers have been recorded at Kachemak Bay and Redoubt Bay (upper Cook Inlet, approximately 110 km northwest of Kachemak Bay) on same day surveys (Gill and Tibbitts, unpubl. data). During our study, seven of the nine Cook Inlet detections were at Kachemak and Redoubt Bays. Peak day shorebird numbers for these two areas were relatively low: fewer than 20,000 shorebirds at Redoubt Bay (1996 only; Bennett, pers. comm.) and fewer than 11,000 birds at Kachemak Bay in both years (West, pers. comm.; Kleinleder, pers. comm.). In contrast, during spring 1997 peak day numbers of more than 150,000 Western Sandpipers were recorded on 10 May in Redoubt Bay (Gill and Tibbitts, unpubl. data). These numbers suggest that use of Cook Inlet by Western Sandpipers varies between years, and 1995 and 1996 may have been low use years.

The migratory route of birds flying past the Copper River Delta is still uncertain. Only 1 of the 17 birds relocated on the YK Delta breeding grounds had been previously detected at Cook Inlet, but we may have missed others because our coverage was not complete. Birds could be using Cook Inlet in large numbers for short periods of time, perhaps only when weather prohibits passage over the mountains. During our study, average length

of stay for birds stopping at Cook Inlet was less than two days (Warnock and Bishop 1998). Within one day's time, birds could fly from the Copper River Delta directly west over the Kenai Peninsula and Cook Inlet, continuing up the Drift River into interior western Alaska (Gill, pers. comm.), a distance of approximately 500 km.

Some Western Sandpipers may overfly Cook Inlet on the way to their breeding grounds. Daily aerial coverage during our two seasons at Kachemak Bay yielded only 3 of 127 radiomarked birds. Furthermore, with the exception of Redoubt Bay, our extensive coverage of northern Cook Inlet (Trading Bay and Susitna Flats) revealed no radiomarked birds. None of the birds detected at Cook Inlet were found in either the Bristol Bay area or the Mulchatna River area. Cook Inlet may serve as a stopover for birds breeding north of the YK Delta. Other studies support this suggestion. Senner and coworkers (1981) detected significant morphometric differences between Western Sandpipers stopping at Cook Inlet (Kachemak Bay) and those stopping at the Copper River Delta. More recently, relocations of Western Sandpipers colormarked at winter sites in Mexico, Panama, and Peru included several resightings of northward bound birds at the Copper River Delta, but none within Cook Inlet (Butler et al. 1996). Clarification of the origin and destination of Western Sandpipers using Cook Inlet requires further study.

Small numbers of Western Sandpipers stop regularly on the intertidal areas in northeastern Bristol Bay. Western Sandpipers are known to breed on the Alaska Peninsula (Gill et al. 1981; Dewhurst, pers. comm.; Kessel and Gibson, pers. comm.), but we detected no radiomarked birds on the Peninsula nor at Cape Peirce the westernmost end of Bristol Bay, where Western Sandpipers breed in low numbers (Winker, pers. comm.). However, our coverage of these areas was limited.

To the east of Bristol Bay, in the Mulchatna River area, we detected three radiomarked birds. It is possible that these birds were late migrants. Egg laying on the YK Delta ranges from 19 May–20 June (Brandt 1943, Gabrielson and Lincoln 1959, Holmes 1972), and these three birds were detected on 29 and 31 May. Peak egg laying on the YK Delta occurs during the last few days of May. However, the three birds we detected on the Mulchatna River area had not been detected at the Copper River Delta since 10 (n = 2) and 15 May (n = 1). Given the rapid rate of travel and quick turnover at stopovers that we have observed in migrating Western Sandpipers (Warnock and Bishop 1998) it seems highly unlikely that these birds would have taken so long to traverse this section of their migration route. In 1997, at New Stuyahok, approximately 70 km southwest of the Mulchatna sightings, Brann and Andres (unpubl. data) recorded Western Sandpipers as possible breeders. We suggest the area around Mulchatna River supports a breeding population of Western Sandpipers. Ground work is needed to clarify this potential breeding range extension.

Our 17 detections of radiomarked Western Sandpipers at interior sites at the YK Delta provide evidence that the YK Delta is the final breeding destination for many of the birds migrating through San Francisco and other Pacific Coast areas. Determination of whether there are significant differences in detections of birds at breeding areas based on their spring banding location is hampered by our small sample sizes and limited coverage. In the two years of this study, we detected only two Honey Lake birds at potential breeding areas: one on the YK Delta and the other at Mulchatna. Honey Lake birds may migrate farther north to breeding areas on the Seward Peninsula, a major breeding area (Kessel 1989) that we did not monitor.

In summary, we have documented a link between coastal and inland stopover sites for Western Sandpipers migrating from San Francisco and Honey Lake, California, and Grays Harbor, Washington, north to breeding grounds on the YK Delta of western Alaska. Our detections suggest that birds departing the Copper River Delta migrate quickly to their breeding areas, with brief intermediate stops. Further studies on the relationships between spring migration routes and specific breeding areas are warranted, especially with an increased search effort of potential breeding areas. These data would complement and expand our understanding of the ecology and evolution of Nearctic migrants.

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BREEDING BIOLOGY OF THE MONK PARAKEET

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ABSTRACT.—The Monk Parakeet (*Myiopsitta monachus*) is unique among parrots because it constructs stick nests rather than nesting in holes. This study provides a detailed description of the species' breeding biology and provides evidence that this species might breed cooperatively. Although many parakeet pairs were observed roosting in solitary nests, breeding occurred only in nests within colonies or chambers within compound nests housing other parakeets. The male was responsible for all or most of the nest construction and maintenance. He fed the female during the incubation and early nestling periods, but later in the nestling period both the male and female fed the nestlings. Most breeding attempts involved a male-female pair, but three separate breeding attempts were made by trios (two trios included a female and two males, and the third trio was composed of a male and two females). In the trios, one of the auxiliary bird contributed less to the breeding effort than the primary male and female. The observations of trios support the idea that Monk Parakeets are similar to cooperative breeders, but the lack of cooperation in nest building indicates that colonial nesting may be a result of other benefits of group living, such as improved predator detection. *Received 7 Jan. 1998, accepted 16 Aug. 1998.*

The social behavior of most parrots has remained unstudied, at least partly because of the difficulty of observing birds that are typically far-ranging and often dwell in forest canopies. Compared to most of its relatives, the Monk Parakeet (*Myiopsitta monachus*) is a relatively tractable species for behavioral study. It is common throughout its range, generally lives in semi-open habitat, and spends a large amount of time in the vicinity of its nests. Monk Parakeets are unusual among parrots for building large domed nests instead of nesting in holes (Forshaw 1989). These nests are built of twigs and may include several chambers, each occupied by a different pair or group of birds. Nests are often clustered in the same or nearby trees to form colonies, and they are used for roosting as well as for breeding (Forshaw 1989). In Bolivia, Monk Parakeets (*M. m. luchsi*) build their stick nests on cliffs rather than in trees (Lanning 1991). The strong tendency to breed colonially, along with delayed breeding, reduced dispersal, and incidental helping led Bucher and coworkers (1991) to suggest that the Monk Parakeet breeding system shares some characteristics with cooperatively breeding species.

The large stick nests built by these parrots are the center of much of their daily activity. They are used year round by breeding as well as non-breeding birds and, while building activity peaks during and immediately following the breeding season (Martella and Bucher 1993), maintenance occurs year round (Bucher et al. 1991). Nests are fully enclosed, domed structures, usually built using thorny twigs (Forshaw 1989). They typically include 1–4 chambers in natural settings, each with its own entrance tunnel (Bucher et al. 1991).

Pairs have been reported to be socially monogamous (Navarro et al. 1995), but the duration of pair bonds is unknown. Nestlings fledge approximately 40 days after hatching (Bucher et al. 1991) and remain with their parents for about three months (Martín and Bucher 1993). Martín and Bucher (1993) did not find any young with their parents in subsequent breeding seasons. However, Emlen (1990) found that in captivity offspring often continued to roost with their parents for up to two years after fledging. These grown young sometimes assisted their parents by bringing food to chicks and possibly incubating.

Work by Bucher and his collaborators (e.g., Bucher et al. 1991; Martín and Bucher 1993; Navarro et al. 1992, 1995) in Córdoba Province, Argentina, has yielded a great deal of information about the basic and population biology of these birds. Here I present the results of a detailed behavioral study of breeding Monk Parakeets. I examine the evidence that the species might be an incipient cooperative breeder, and that the compound nests com-

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monly built by Monk Parakeets represent an important form of cooperation.

METHODS

Study area.—During the Austral spring and summer (September–January) of 1993–1994 and 1994–1995, I studied the breeding behavior of Monk Parakeets in northern Entre Ríos Province, Argentina. The region receives approximately 1200 mm annual rainfall (Rojas and Saluso 1987), mostly during the spring and summer months (A. Ortíz Basualdo, unpubl. data). Mean annual temperature is approximately 19° C, with summer (January) and winter (July) means of 26° C and 12° C, respectively (Rojas and Saluso 1987).

My study area encompassed an approximately 1000 ha uncleared portion of Estancia Santa Ana de Carpinchorí (58° 45′ W, 31° 25′ S), a 5508 ha cattle ranch near the town of Federal. Parts of Estancia Santa Ana have been cleared, but much of it is savannah woodland, dominated by three xerophytic trees: *Acacia caven, Prosopis affinis,* and *Prosopis nigra.* Additional trapping of birds was done at Estancia Palmira, a 4974 ha ranch that adjoins Estancia Santa Ana. During the years preceding 1992, parakeets on the ranches had been subject to annual control measures (poisoning and burning of nests) that are required by law in the area. These control efforts were suspended 1992–1995 throughout the study.

Observations.—At the beginning of each field season, I located all nests in the study area by riding through the area on horseback and interviewing the ranch hands. Throughout the season, I monitored the occupancy and breeding activity of all nests that were accessible with a 7-m ladder.

Observations (2–3 hours every 3–4 days) were initially made at all nests to select focal nests, which were those occupied by birds that showed signs of breeding. Focal nest observations were made at three day intervals (mean = 3.0, ± 1.08 SD days) in 1993-1994, and every 3.2 ± 1.29 days in 1994–1995. Each focal nest observation lasted an average of 220 ± 58 min in 1993-1994 and 147 ± 15.5 min in 1994–1995. Nests that were used primarily for roosting (i.e., birds were seen there only early in the morning and late in the afternoon) were visited less frequently. I increased the frequency of observations if the birds showed signs of breeding. I made observations for a total of 606.25 h in 1993–1994, and 623.75 h in 1994–1995, with 305 h and 491.5 h respectively focused on nests of breeding birds.

I followed a rotating observation schedule so that the time (early morning, mid-morning, early afternoon, mid-afternoon) of observations was varied systematically for all nests. Weather permitting, observations began at sunrise and continued until middle or late afternoon (16:00–17:00 local time). All observations were made from 15–30 m away (birds quickly became habituated to me), with the aid of 7 × 35 binoculars and/or a 15–45 × 60 zoom spotting scope. The activity and location of all focal birds (2–6, depending on the number of pairs breeding in the focal nest or nests) were recorded every two minutes in a notebook, along with other observations (e.g., arrivals and departures, aggressive and affiliative interactions, building activity, etc.). While observing focal birds, I recorded the size of groups (including "groups" of one bird) that flew past, and also recorded the sizes of groups seen while I rode to or from observation sites. Observations were suspended during rainstorms because the birds did little more than sit. Observations were not made at nests whose occupants I had attempted (successfully or unsuccessfully) to trap on the previous night.

Only breeding males' and females' nest building are compared here. I quantified nest building and maintenance in three ways: number of twigs added per hour, number of minutes per hour spent adjusting/rearranging twigs, and number of minutes per hour spent shredding twigs. This final activity involves chewing twigs into small pieces that are used to line the nest chamber. Although I usually couldn't observe the activity, it was clearly audible. To avoid pseudo-replication, I pooled breeding attempts for pairs that were observed during more than one attempt, thereby yielding one set of data per breeding pair.

For the time-budget analyses of breeding behavior, the observations from multiple breeding efforts were similarly pooled, and trios were excluded from the analysis. Time-budget estimates were broken down into three time periods: pre-laying (the 10-days prior to clutch initiation), laying, and post-laying (the 10 days following completion of egg-laying). In calculating the proportion of time that the male and female were together, I assumed that the pair was together only if I saw them leave and arrive together. The female was considered to be alone only if I knew where she was and knew that the male was gone, or vice versa. If both were gone from the nest area, but left and/or arrived at different times, the time interval was excluded from the analysis. Individuals were considered to be in the nesting area if they were within 100 m of the nest.

Trapping, marking and sex identification.—Parakeets were trapped at night as they roosted in their nests, using a modified, light-weight version of the trap designed by Martella and coworkers (1987; see Eberhard 1997). Captured birds were held overnight in numbered cloth bags. At daybreak they were banded, weighed, and a blood sample (approximately 50–100 μl) was taken from the brachial vein. The blood was immediately placed in 1.25 ml of lysis buffer (0.1 M Tris, 0.1 M EDTA, 2% SDS, pH 8.0) and later frozen. Colored anodized aluminum leg bands (Gey Band and Tag Co.) were used to mark the birds for individual identification. Immediately after being processed, birds were released within 300 m of their nests. To avoid disturbing birds that were in the process of settling into a nest, individuals sometimes were temporarily marked using dyes (Rhodamine B or Malachite Green, Sigma Chemical Co.). This was accomplished by mixing a saturated dye/alcohol solution with petroleum jelly; the dye-impregnated jelly was then dabbed on the nest en-

trance and birds dyed themselves as they passed through the opening.

Because Monk Parakeets are sexually monomorphic [Forshaw 1989; or "similar" according to Juniper and Parr (1998), who do not provide distinguishing characters], a sex-specific DNA probe (Zoogen, Inc.) was used to identify the sex of individuals in the study. The blood sample taken at the time of banding was used as a source of DNA, which was later extracted in the lab. Since the lab work was done after conclusion of each field season, behavioral observations were made without knowledge of the focal individuals' sex. Total genomic DNA was extracted from each sample and digested using a restriction enzyme (either TaqI or BamHI). Restriction digests were run out in agarose gels and transferred to nylon membranes by Southern blotting. Blots were probed by Zoogen, Inc., Davis, California to identify the sex of each individual. All the 1993–1994 samples were digested with TaqI, which revealed an alternate Z allele that made sex determination of some individuals ambiguous. For this reason, samples of those individuals' DNA were reprocessed using BamHI, which yields more consistent, dependable results. All of the 1994–1995 samples were digested with BamHI and no unusual alleles were detected. A more detailed description of laboratory protocols can be found in Eberhard (1997).

Nest checks.—Nest checks were begun once a female appeared to be incubating (i.e., once she began spending most of her time in the nest). The eggs were counted and a second egg count was made about 10 days later. At both of these egg checks, the eggs were numbered with indelible ink to facilitate the detection of future laying and egg disappearances. The nest was checked again when I estimated that all of the eggs should have hatched, and again about two weeks later, at which point the nestlings were banded and blood samples taken. Since Navarro and coworkers (1991) did not detect a negative effect of visiting nests every 10 days, I am confident that my less frequent visits did not adversely affect the breeding of birds in this study.

RESULTS

Sexes and weights of banded birds.—Eighty-five parakeets (56 adults and 29 nestlings) were banded at Estancia Santa Ana and another 50 (27 adults and 23 nestlings) were banded at adjoining Estancia Palmira. In the 1993-1994 field season, I attempted to trap and band all occupants of accessible nests at the start of the field season. During my second field season I trapped only focal birds, and did so only after the female had begun to lay.

Because the 1993–1994 sample of banded birds is a cross-section of the birds in the study area (not biased toward breeding pairs as the 1994–1995 sample is), it can be used as an indicator of the sex ratio of the adult population in the Santa Ana and Palmira area. Of the 60 adult birds whose sex was determined, 30 were females and 30 males. The sex ratio of nestlings banded during both field seasons was almost equal: pooling the nestlings from both Palmira and Santa Ana, there were 27 females and 23 males. Weights of adult males (114.9 ± 7.19 g, n = 37) and females (114.8 ± 10.49 g, n = 39) were almost identical.

Nest locations.—During the two field seasons, I monitored 39 nests that were occupied for at least part of the study; I was unable to access 3 of them for regular nest checks, so they are excluded from the analysis of breeding behavior. The nests included 67 chambers (62 in the accessible nests), and had a mean of 1.8 ± 2.1 chambers per nest. Most of the nests that I monitored were built in *Prosopis nigra* trees, the tallest of the three native trees that dominate the study area. There were three colonies with nests built in the *Eucalyptus* sp. trees lining the ranch entrance, but only two nests from two of these colonies were included in my study because the others were too high to reach. One nest in the study was built on the cross-bar of a utility pole. Details about the sizes and locations of monitored nests are listed elsewhere (table 3.1 in Eberhard 1997).

Twenty-five nests were in colonies and 14 were solitary. Solitary nests are defined as those with nearest neighbors at least 100 m away. This definition follows from the distribution of nearest-neighbor distances shown in Fig. 1 and is consistent with Bucher's and coworkers' (1991) use of the term "colony", a term equivalent to Hyman's and Pruett-Jones' (1995) "nesting area." Nests from 7 colonies are included in the sample. While I use "colony" to denote a group of nests, it is important to note that each nest itself can contain several chambers. On two occasions I found more than one pair breeding in isolated multichambered nests and did not consider the pairs to be solitary breeders.

Nest building.—Nest construction and maintenance was observed throughout the breeding season by both breeding and nonbreeding birds. Parakeets at Santa Ana used the thorny terminal twigs of three tree species common in the area (*Acacia caven, Prosopis affinis,* and *P. nigra*). Most of the twigs were clipped from trees within 100 m of the nest.

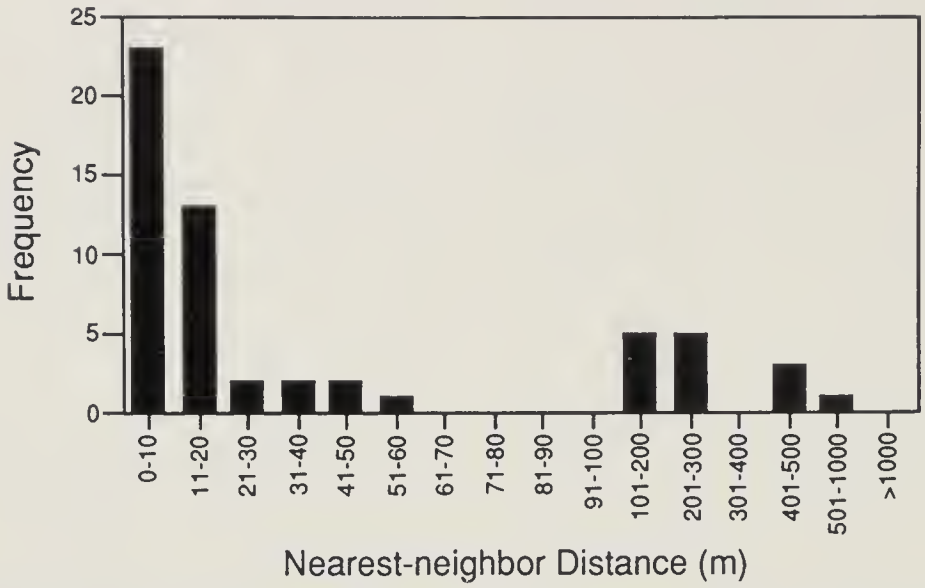

FIG. 1. Histogram of nearest-neighbor distances for all Monk Parakeet nests (both monitored and non-monitored; n = 57 nests) in the Santa Ana study area.

Some males stole twigs from neighboring nests or from parts of the compound nest away from the individual's compartment, often from occupied nests while the occupants were away. On average, 2% (range 0–8%) of the twigs added to nests were stolen ones. When building on a compound nest, twigs were always added to the individual's part of the nest; when adding to the roof, twigs were added only above the individual's chamber. Half of the 39 monitored nests had originally been built by Brown Cacholotes (*Pseudoseisura lophotes*) and subsequently remodelled by parakeets (J. Eberhard 1996).

The construction of new chambers often accompanied the initiation of a breeding attempt. Of 19 breeding attempts, 7 (37%) began with the construction of a new compartment. Only one of these new compartments constituted a new nest; all others were additions to existing nests. On four occasions, I observed pairs build a new compartment but not use it for breeding. Three of these four pairs moved out of their new nest (only one of these pairs was resighted later); the fourth continued to use the new compartment, but did not breed.

Males added more twigs than females (Wilcoxon test: $Z = -2.934$, $P = 0.003$, $n = 11$ pairs). Often, while the male was busy adding twigs to the nest, the female perched quietly nearby or inside the nest. When construction began, the female sometimes perched where the chamber would eventually be and the male built around her. Males spent significantly more time adjusting and rearranging twigs on the nest (Wilcoxon test: $Z = -2.847$, $P = 0.004$, $n = 11$ pairs) than females. On the other hand, females spent significantly more time shredding twigs to line the nest chamber (Wilcoxon test: $Z = 2.032$, $P = 0.042$, $n = 11$ pairs).

The rate of nest-building (twig addition + twig rearrangement + twig shredding) activity was higher early in the breeding attempt. To test this, I compared nest building and maintenance rates during the 10-day period before egg laying began with the 10-day period after egg laying had been completed. Two breeding attempts by two different pairs were omitted from this analysis because no prelaying data were available for them. The mean percentage of time spent in nest building and maintenance during the prelaying period was 10.0% for males and 2.8% for females; during the postlaying period, these values dropped to 3.9% and 0.6%. Both males and females spent a greater proportion of time on nest-building and maintenance during the prelaying period compared with postlaying (Wilcoxon tests: $Z = -1.965$, $P = 0.049$ and $Z = -2.158$, $P = 0.031$, respectively; $n = 17$ breeding attempts). When pairs' multiple breeding attempts were pooled, this increased building effort was not detectable, possibly because of small sample sizes. In this pooled comparison, pre- and postlaying nest building and maintenance rates were not significantly different

for males or females (Wilcoxon tests: Z = −1.580, $P > 0.05$ and Z = −1.660, $P > 0.05$, respectively; n = 10 pairs).

Defense of the nest.—In general, Monk Parakeets were quite tolerant of having other birds (both conspecifics and other species) near their nests. During both breeding seasons, I observed 186 chases by members of breeding pairs. Males and females did not differ in the number of chases that they made (Wilcoxon test: Z = 0.178, $P > 0.05$, n = 10 pairs). On average, parakeets chased birds that were 3.0 m (±3.1 m, n = 186 chases) from their nest, with no difference between males and females (Wilcoxon test: Z = −0.700, $P > 0.05$, n = 10 pairs). Other species were allowed closer (1.96 m) than parakeets (3.07 m) before being chased (Kolmogorov-Smirnov test: D = 0.463, P = 0.011, n = 186 chases).

The American Kestrel (*Falco sparverius*) and the Speckled Teal (*Anas flavirostris*) nested in Monk Parakeet nests at Santa Ana. Kestrel pairs took over two different compound nests during the study, and ducks nested in three of the monitored compound nests, using chambers that were not being used by parakeets.

Travelling groups.—When away from their nesting areas, parakeets generally traveled in small groups (mean = 2.98 ± 2.83 birds; range 1–30, n = 777 groups), but included more than one bird 87.5% of the time. As they left the nesting area, focal birds often joined other birds. I analyzed the departures of each focal pair separately (pooling multiple breeding attempts). In a total of 1893 departures by the members of 11 breeding pairs, over a quarter of the time (27.1 ± 10.1%) focal birds left the nesting area with other parakeets. On average, the groups they joined were composed of 2.0 ± 0.9 other birds. Neither the percentage of the departures that were with other birds, nor the size of departure groups, were correlated with the number of birds in the colony (Spearman rank correlation: r_s = 0.243 and r_s = 0.178, respectively; $P > 0.05$ for both cases).

Breeding groups.—Most of the breeding attempts I observed involved male-female pairs. However, on three occasions I observed breeding attempts by trios. Two of these included one female and two males, while the third trio was composed of one male with two females. In the 35 nests (62 compartments) that I could access for regular nest checks, I observed 7 breeding attempts by 4 pairs and 2 trios in 1993–1994, and 12 breeding attempts by 8 pairs and 1 trio in 1994–1995. Of the six 1993–1994 breeding groups, four were followed in 1994–1995 also. At the beginning of the 1994–1995 field season, all four occupied the same compound nest they had occupied at the end of the previous season. In three of the four cases, the pair had moved to a new compartment. The other pair moved 600 m to a different colony following an unsuccessful breeding attempt in 1993–1994. The fact that the four breeding pairs followed during both seasons remained together suggests that Monk Parakeet pair bonds are long-lasting.

One 1993–1994 trio (a female with two males, FMM) disappeared from the study area after its nest was blown down by a storm during the incubation period. The other FMM trio was observed through the building, incubation, and nestling periods in 1994–1995. In both of these trios, one of the males (the "primary" male) was a more active participant in the breeding effort. During the incubation period, the primary male consistently went into the nest chamber after returning from an absence, presumably to feed the female; the auxiliary male returned less often, and usually sat outside the nest upon returning. Occasionally, the auxiliary male spent extended periods sitting in the nest with the female. Since I was rarely able to observe activity within the nest, I could not quantify the rates at which males fed females. However, on one occasion the female from one of the trios emerged from the nest and both males fed her. I observed little building by the first trio, and both males' effort was approximately equal. Both males in the second trio collaborated in the initial construction of a new nest compartment, but later maintenance was all done by the primary male. One full-length copulation was observed between the two males in the first trio, who were 4 m from their nest in which the female was incubating.

The third trio (MFF) began its breeding attempt at the end of my 1993–1994 field season, so it was observed only during the building and incubation stages. All three birds participated in the construction of a new nest chamber that was quickly added to an existing

compound nest. One of the females (the "primary" female) assumed the task of incubating the clutch of 5 eggs. Once while the primary female was incubating, the male attempted to copulate with the auxiliary female 0.5 m from the nest but was rejected with lunges and biting.

Copulations.—Monk Parakeet copulations are prolonged and may include several mounts by the male. These series of mounts are best termed "copulation bouts" (Birkhead and Møller 1992). I observed a total of 31 successful copulation attempts and 14 unsuccessful ones. Following Snyder and coworkers (1987), a copulation attempt was considered successful if cloacal contact was clearly made. Because my observations were focused on nests, most of the copulations I saw were by the resident birds, but I observed a few copulations by non-resident birds, indicating that pairs also copulate away from their nests. The observed copulations occurred an average of 23 ± 79.2 m from the pair's nest (range 0–410 m, n = 44 pairs). Six of the copulations took place inside nests and is likely an underestimate because it was difficult to observe activity within the nest.

Copulation bouts usually (33 of 45, or 73%) began with the male "head-shaking" (the bird ruffled up its head feathers slightly and gave its head quick shuddering shakes, raising its head slightly with each series of shakes) and sometimes strutted back and forth on his perch with very deliberate steps. Females would sometimes head-shake as well (18 of 45, or 40%). Males were more likely to initiate a copulation bout than females. Of 28 bouts in which one individual clearly initiated the interaction, 21 (75%) were initiated by the male. Occasionally the female mounted the male briefly as the copulation bout began. During his mounts, the male placed one foot on the female's back and brought his tail under hers, bringing his cloaca against hers. All the while, the male waved his tail back and forth as he pressed his cloaca against hers and sometimes held his beak open or gently grasped the female's beak. The male usually dismounted a few times to head-shake or move to the other side of the female, so a single copulation bout often involved several different mounts by the male. Successful copulations often ended with the male pressing his cloaca more firmly against the female's for one or two seconds, after which he climbed off. In 16 copulation bouts for which I was able to determine which bird had terminated the copulation, it was usually (12 times, 75%) the male who simply stepped off. In four (25%) bouts, the female ended the copulation by putting her tail down or moving away. A successful copulation bout required the female's cooperation, and clearly it was easy for her to end it; no forced copulation attempts were observed.

The average duration (from the beginning of the first mount to the end of the last) of successful copulation bouts was 274 seconds (range: 60–480 s, n = 31). In 19 of these bouts I measured the time that the male was actually mounted, as well as the total duration of the copulation bout. Males spent an average of 159 ± 53 seconds mounted (range: 30–263 sec, n = 19), which represents an average of 71% of the copulation bout (range: 47–100%, n = 19). Three copulation bouts included single mounts that ranged 60–120 seconds.

Mate guarding.—Because Monk Parakeets breed in colonies, they might be expected to engage in extra-pair copulations, and males to mate guard (Birkhead and Møller 1992). Comparing the percentage of time that the male spent with the female and the percentage of time the female was alone during the egg-laying period and the postlaying period, I found no difference in the proportion of time that the male and female were together (Wilcoxon test: $Z = -0.533$, $P > 0.05$, n = 10 pairs) or that the female was alone (Wilcoxon test: $Z = 0.561$, $P > 0.05$, n = 10 pairs) during the laying and post-laying periods. Therefore, there is no evidence that males guarded their mates during their fertile period.

Begging and allofeeding by breeding birds.—Egg-laying was accompanied, and often preceded, by an increase in the frequency with which females begged their mates for food. The females' begging behavior was like that of young birds and often a begging call (see Martella and Bucher 1990) was given. Females were sometimes extremely insistent in their begging when the male was in the nest area. Adult males were never seen begging or heard making begging calls.

Begging by the female was strongly associated with egg-laying: the begging rate (min/h) during the prelaying and laying periods

TABLE 1. Breeding statistics for the 1993–1994 and 1994–1995 breeding seasons at Santa Ana (SA). Following Navarro et al. (1992), hatching success is defined as #nestlings/#eggs, fledging success is #fledglings/#nestlings, and breeding success is #fledglings/#eggs. Several clutches laid late in the season were not included in SA success calculations because they were due to hatch/fledge after the end of the field season: 93–94 (two clutches) and 94–95 (two clutches).

	SA 93–94	SA 94–95	$\bar{x}_{SA}$	$\bar{x}_N$[a]	Range$_N$[a]
# occupied chambers	27	29	28	52.1	38–78
% chambers with eggs	22.2	30.0	26.1	60.0	37–91
Mean size of first clutches	4.3	5.2	4.8	5.6	5.1–6.1
Hatching success (1st clutches)	0.3	0.6	0.4	0.6	0.5–0.7
Fledging success (1st clutches)	0.0	0.7	0.4	0.4	0.1–0.6
Breeding success (1st clutches)	0.0	0.4	0.2	0.3	0.04–0.4
% successful first clutches	0.0	62.5	31.3	43.7	14–53
% pairs re-laying	16.7	33.3	25.0	14.6	8–29
Mean size replacement clutches	4.0	5.0	4.5	4.6	4.0–5.1
Hatching success (rep. clutches)	0.0	0.2	0.1	0.4	0.2–0.5
Fledging success (rep. clutches)	0.0	1.0	0.5	0.4	0–1.0
Breeding success (rep. clutches)	0.0	0.1	0.0	0.2	0–0.4
% successful rep. clutches	0.0	50.0	25.0	29.0	0–67
Overall productivity per pair	0.0	1.8	0.9	1.5	0.5–2.3
Overall prod./occ'd chamber	0.0	0.6	0.3	0.9	0.4–2.0

[a] Summary means and ranges of yearly means of data from a 7-year study of Monk Parakeets in Córdoba, Argentina (N; Navarro et al. 1992).

combined was significantly greater than the begging rate for all other times combined (Wilcoxon test: $Z = -2.803$, $P = 0.005$, $n = 10$ females). Males responded to this increased begging by increasing rates of allofeeding (bouts/h). The rate at which males fed females was significantly greater before and during egg-laying compared with the allofeeding rate at other times (Wilcoxon test: $Z = -2.201$, $P = 0.028$, $n = 10$ males). Females were never seen allofeeding their mates.

Egg-laying and incubation.—Incubation began when the first egg was laid and was only by the female. During the laying and incubation periods, males returned every 1–2 hours, presumably to feed the female. Generally I was unable to observe activity within the nest chamber, but occasionally caught glimpses of or could hear the female being fed. On only two occasions (two different pairs) I saw the female emerge from the nest to be fed outside. Females sometimes left the nest during the incubation period to feed, to collect small twigs, to stretch, to chase away intruders, or because of a disturbance. Males spent time inside the nest during the laying and postlaying periods (16% and 24% of their time, respectively), but always with the female and did not appear to relieve her from incubation duty.

Care of the nestlings.—Females continued to spend much of their time in the nest after the eggs hatched, leaving the nest more frequently and for longer periods of time as the nestlings grew. Since I was unable to observe activity within the nest chamber, and since both the male and female often entered the nest together, I could not quantify the feeding of young by males or females. It was clear that once she began leaving the nest, the female contributed to the feeding of nestlings. The nestlings usually fledged all at once, and thereafter spent little time in the nest. Most of the families with fledglings spent little time in the nest area (and when they did, were often hidden in the tree tops), so I was unable to observe many interactions between parents and offspring, and among offspring.

Breeding statistics.—Breeding in 1993–1994 began later than in 1994–1995, fewer pairs made breeding attempts, and none of those pairs was successful (Table 1). In 1993–1994, 22.2% of 27 the occupied chambers were used for breeding, and in 1994–1995 31% of 29 were used (this difference was not significant; $\chi^2 = 0.583$, df = 1, $P > 0.05$).

The mean clutch initiation date for 1993–1994 was 16 November, while the mean date for 1994–1995 was 26 October; this difference in clutch inititation date is not statistically significant (Kolmogorov-Smirnov test:

D = 0.500, $P > 0.05$, $n = 15$ first clutches). First clutches at Santa Ana contained an average of 4.8 eggs (range 3–7 eggs, $n = 15$); sizes of replacement clutches were not significantly different (4.5, range 3–7 eggs, $n = 4$ clutches; Mann-Whitney U-test: Z = −0.300, $P > 0.05$, $n = 19$ clutches). Overall, clutch sizes at Santa Ana tended to be smaller than those observed by Navarro and coworkers (1991; Table 1).

Hatching success (number of nestlings/number of eggs laid) for first and replacement clutches combined was significantly greater during the 1994–1995 breeding season than in 1993–1994 ($\chi^2 = 4.59$, df = 1, $P < 0.05$). Similarly, breeding success (number of fledglings/number of eggs; clutches due to fledge after the end of the field season were excluded) was significantly greater during 1994–1995 ($\chi^2 = 11.86$, df = 1, $P < 0.001$). Hatching and breeding success during 1993–1994, but not 1994–1995, at Santa Ana was lower than during any of the seven years of Navarro's and coworkers' (1992) study.

Predation and failure to hatch were the two most common causes of nest failure. Predation was never observed, but potential predators that were resident in the study area included snakes, opossums (*Didelphis virginiana* and *Marmosa agilis*), and kestrels. In all 4 cases of presumed predation, the nest itself was intact, and the adults were seen in the area later. The five complete hatching failures were restricted to two pairs, one of which was followed during both years. During the second field season, I opened or candled all unhatched eggs, and in the case of these two pairs, all unhatched eggs appeared to be infertile.

DISCUSSION

In their overview of Monk Parakeet biology, Bucher and coworkers (1991) suggested that Monk Parakeets show some characteristics that are typical of communally (i.e., cooperatively) breeding species. As outlined by Brown (1978), the most important feature of communal breeding systems is that helpers are regularly involved in the care and feeding of young. These helpers are generally individuals who defer breeding, so the evolution of helping behavior is "inextricably bound to the evolution of delayed breeding" (Brown 1978: 125).

Martín and Bucher (1993) found that Monk Parakeets delay breeding at least two years, and 50% wait longer. One of the most striking results from my study at Santa Ana was the finding that some breeding attempts involved trios. Emlen (1990) observed trios in a captive colony of Monk Parakeets, but the present study provides the first documentation of Monk Parakeet trios in the wild. While male-female pairs are the most common breeding unit, trios do not appear to have been an anomaly because they were observed during both years at Santa Ana. Bucher and coworkers (1991) observed incidental helping in the form of allofeeding: older fledglings fed their younger siblings, a non-breeding trio fed fledglings from a neighboring nest, and a breeding bird fed a begging juvenile from a neighboring nest. However, the low level helping observed in this study (like that observed by Emlen) occurred as a part of long-term associations that lasted through the breeding season. At Santa Ana both male and female auxiliary birds were observed assisting in nest-building and maintenance, feeding the incubating female, and possibly by watching for predators while they accompanied the incubating female. In the case of the trio with a female auxiliary, there was no evidence that she layed eggs; the group's clutch size was within the range of clutch sizes observed for other pairs in this study. The trios observed by Emlen (1990) involved a breeding pair's young (of unknown sex) from the previous breeding season. In the case of the Santa Ana trios, the identity and relatedness of the auxiliary to the breeding pair was unknown. Also unknown is the impact of the auxiliary bird's presence on the success of a breeding attempt.

A second form of helping described by Bucher and coworkers (1991) involves cooperation in the construction of nests, but my observations suggest that nest building was anything but cooperative. While the addition of a new chamber onto an existing nest appeared to facilitate construction, I did not see any clear cooperation among members of different pairs in nest-building. Twig theft (which sometimes involved an individual stealing twigs from areas of its compound nest away from its own chamber) was not unusual, and when building on a compound nest, an individual clearly focused its building on the

area of the nest immediately around its own chamber. Therefore, nest building does not appear to be a cooperative effort where various members of a compound nest collaborate to build a structure [such as the roof by Sociable Weavers (Collias and Collias 1984)] from which they all will benefit. Rather, multi-chambered nests seem to result from the convenience of adding chambers to existing nests compared with building nests from scratch.

The tendency for Monk Parakeets to nest in groups does not appear to result simply from attempts to reduce building effort by adding chambers onto existing nests. Most nests are small (<4 chambers), but built near one another in the same or adjacent trees. There is probably a trade-off between the benefits of reducing building effort and the cost of potential nest loss. Nests are typically built on the ends of rather thin branches, and large nests are more likely to fall during windstorms. Birds at Santa Ana showed a clear preference for breeding in colonies (no solitary breeders were found); solitary nests, which were often adopted cacholote nests, were used only as roosts (J. Eberhard 1996). My sample sizes were too small to examine the effect of colony size on breeding success. Navarro and coworkers (1992) did not find a statistically significant effect of communal nest size on productivity of a nest chamber. However, the grouping that occurs at the scale of colonies may be more important than grouping into compound nests, so a re-analysis of their data to examine the effect of colony size (instead of nest size) on productivity might be more relevant.

Potential advantages to Monk Parakeets breeding in colonies include increased ability to detect predators, group defense (Hoogland and Sherman 1976), and improved foraging efficiency (Ward and Zahavi 1973). Improved detection of predators could be especially important for incubating females because they are confined and cannot look out for predators. An approaching predator is announced with alarm calls by any parakeet in the area. Consequently, a female incubating in a colony is more likely to be alerted and leave her nest than a solitary female. This element of safety could explain the tendency of Monk Parakeets to breed in colonies rather than in isolated nests. The abundance and relatively uniform distribution of food at Santa Ana during the breeding season (pers. obs.) suggests that colonial nesting is not likely to improve foraging efficiency. The lack of correlation between colony size and percentage of departures with other birds is consistent with this idea. In the autumn, when the parakeets earn their reputation as pests by descending on grain crops, food could be more patchily distributed and colonial roosting could hold a foraging advantage.

The most important correlate of breeding success found by Navarro and coworkers (1995) was laying date. Clutches laid early in the season were larger, produced more nestlings, and consequently more fledglings. This negative correlation between clutch initiation date and breeding success may explain the failure of pairs that attempted to breed during 1993–1994 at Santa Ana. The mean clutch initiation date that year was later than any of the mean clutch initiation dates recorded by Navarro and coworkers (1992) during their seven-year study at approximately the same latitude.

Although there are few detailed behavioral studies of wild parrots with which to compare this one, many of my observations appear to be typical of parrots. The finding that pairs persist for multiple breeding seasons fits the pattern of long-term pair bonds found in Puerto Rican Amazons (*Amazona vittata*; Snyder et al. 1987), the Galah (*Eolophus roseicapillus*; Rowley 1990), Spectacled Parrotlets (*Forpus conspicillatus*; Garnetzke-Stollmann and Franck 1991), *Agapornis* (Dilger 1960), and to some extent, Green-rumped Parrotlets (Waltman and Beissinger 1992). Incubation by the female and maintenance feeding of the sitting female by the male has also been reported for Puerto Rican Amazons (Snyder et al. 1987) and Galahs (Rowley 1990). Increased begging by the female associated with breeding has been noted in Yellow-shouldered Amazons (*Amazona barbadensis*; Sanz and Grajal 1998). In Galahs, head-bobbing (a component of begging) is part of the pre-copulatory behavior (Rowley 1990).

Monk Parakeet copulations are very similar to those described for *Agapornis* lovebirds (Dilger 1960) and Galahs (Rowley 1990). Compared with most birds whose copulations generally last less than 15 s (Birkhead and

Møller 1992), parrot copulations are remarkably long (range of mean durations: 30 sec. to >100 min.; Dilger 1960, Low 1992, Rowley 1990, Skeate 1984, Snyder et al. 1987, Waltman and Beissinger 1992, Wilkinson and Birkhead 1995). At least in the cases of Green-rumped Parrotlets (S. Beissinger, pers. comm.) and Thick-billed Parrots (D. Lanning, pers. comm.), copulations involved single mounts. The duration of Monk Parakeet copulation bouts, as well as some of the single mounts observed, are within the range of copulation times reported for other parrots. The function of these long copulations is not known, but they may be part of courtship (W. G. Eberhard 1996).

Monk Parakeets and species of *Agapornis* (which includes the only other parrots that construct nests) differ somewhat in their division of labor associated with nest-building and maintenance. In Monk Parakeets, the bulk of the nest building is done by males, and females shred twigs to line the nest cavity. In *Agapornis,* both cavity lining (in the species that don't build nests) and construction (in the nest building species) is the responsibility of females (Dilger 1960). This difference could be a result of the way in which nest building evolved in the two genera (Eberhard 1997). The construction of nests in the more recently derived species of *Agapornis* evolved from the habit of nest lining, which is done by the females of species that are basal in the *Agapornis* phylogeny (Eberhard 1998). A possible explanation for the male's predominant nest building role in Monk Parakeets is that this allows the female to conserve energy reserves for egg production.

In summary, the breeding behavior of Monk Parakeets is generally similar to that of other parrots for which comparable observations are available. The major differences are the nest building and maintenance associated with using stick nests instead of holes, the strong tendency to breed in colonies, and the occurrence of breeding trios. Further information about the frequency of breeding trios, the relatedness between breeding pairs and their auxiliaries, and genetic relationships between trios and their nestlings, would all be important in testing the idea that the Monk Parakeet mating system includes features that are characteristic of cooperative breeding systems. Though nest building itself does not appear to be cooperative, the construction of nests in lieu of nesting in holes probably permits individuals to form colonies. Roosting and breeding in colonies could in turn facilitate long term social associations throughout the year, allowing offspring to maintain close contact with their parents during subsequent breeding seasons and perhaps engage in helping.

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LANDSCAPE AND FINE SCALE HABITAT ASSOCIATIONS OF THE LOGGERHEAD SHRIKE

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ABSTRACT.—This study was conducted to determine landscape and fine-scale vegetative variables associated with breeding Loggerhead Shrikes (*Lanius ludovicianus*) on Fort Riley Military Reservation, Kansas. Because Fort Riley is an Army training site, the influences of training disturbance to the vegetation, and range management practices on bird habitat patterns were also investigated. Breeding birds were surveyed in 1995 and 1996 using point counts. Survey plots were identified, *a priori*, at the landscape scale as either grassland, savannah, or woodland edge according to cover by woody vegetation. In 1996, fine-scale habitat at survey points and at bird use sites was measured and a principal components analysis used to characterize the fine-scale herbaceous vegetation structure. A military disturbance index was developed to quantify the severity of vehicle disturbance to the vegetation at survey and bird use sites. Shrikes were associated with savannah habitat at the landscape scale. Sites used by Loggerhead Shrikes were characterized at the fine-scale by tall, sparse, structurally heterogeneous herbaceous vegetation with high standing dead plant cover and low litter cover. At the fine-scale, tree and shrub density did not differ between sites used and not used by shrikes. Used sites did not differ from survey sites with respect to military training disturbance, hay harvest, or the number of years since a site was last burned. Our results in this study suggest that the shifting mosaic of vegetation on Fort Riley resulting from training and range management practices maintains adequate habitat for breeding shrikes. *Received 25 Sept. 1997, accepted 18 June 1998.*

Declines in numbers of Loggerhead Shrikes (*Lanius ludovicianus*) have been reported for most areas of the United States and for western Canada (Arbib 1976, 1977, 1978, 1979; Cade and Woods 1997; Kridelbaugh 1981; Morrison 1981; Telfer 1992). In Kansas, the Loggerhead Shrike is designated as a "Species in Need of Conservation" (Kansas Department of Wildlife and Parks 1986). While reasons for the continued decline of Loggerhead Shrike populations remain unclear, loss of breeding and/or wintering habitat is a probable cause (Kridelbaugh 1981, Smith and Kruse 1992).

Shrikes in the eastern U.S. are associated with pastures of relatively short vegetation that offer adequate foraging and perching sites such as utility wires or isolated trees (Bohall-Wood 1987, Brooks and Temple 1990, Smith and Kruse 1992, Telfer 1992, Yosef and Grubb 1993). Management recommendations resulting from these studies have been to provide short grassy habitat interspersed with scattered elevated perches. These recommendations may not be applicable to shrikes breeding in non-agricultural systems.

The structure of herbaceous vegetation in areas of extensive agriculture and grazing is relatively simple and homogenous. As a result, quantification of habitat in the above studies was restricted to percent cover of broad habitat types such as pastures or row-crops (Bohall-Wood 1987, Brooks and Temple 1990). Native grasslands exhibit greater structural heterogeneity, and shrikes breeding in these areas may reveal different or more complex habitat association patterns (Prescott and Collister 1993, Chavez-Ramirez et al. 1994). Native grassland may provide suitable and adequate perch sites for foraging shrikes in the absence of powerlines, fences, or other artificial perching substrates (Chavez-Ramirez et al. 1994).

The structure of herbaceous vegetation within a grassland may be very different depending on how often it is disturbed by burning, grazing, or, in the case of Fort Riley, by military vehicles. Unburned tallgrass prairie is structurally heterogeneous because of the interspersion of standing dead vegetation, forbs, and woody vegetation. Cover and depth of residual litter can be quite high in unburned prairie. Annual fire in the absence of grazing tends to favor dense, homogenous cover by warm season grasses (Gibson 1989), but periodic early spring burns such as those implemented on Fort Riley eliminate litter and in-

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FIG. 1. Location of Fort Riley Military Reservation, Kansas, USA (A). Location of areas of restricted public access at Fort Riley Military Reservation, Kansas, USA (B). Access is limited in the Multipurpose Range Complex, shaded area in northwest, and is never available in the Impact Zone, the shaded area in the center of the fort. The shaded areas in the south are containment areas. We placed the census points (circles) in tallgrass prairie habitat where access was most available.

crease cover by perennial forbs (Anderson et al. 1970). Military disturbance has been shown to increase bare ground and cover by annual and warm season forbs (Johnson 1982, Shaw and Diersing 1990), contributing to an increase in structural heterogeneity.

This study was developed with three major objectives: (1) to determine the habitat associated with breeding Loggerhead Shrikes in tallgrass prairie at both the fine-scale (the scale of habitat within individual territories) and the landscape scale (the scale of the study area); (2) to determine if a relationship exists between the intensity of military training disturbance to the vegetation and habitat associated with Loggerhead Shrikes; and (3) to provide recommendations for the proactive management of shrikes at Fort Riley Military Reservation.

STUDY AREA AND METHODS

Fort Riley, located in Riley and Geary counties in the Flint Hills of northeastern Kansas (Lat 39° 15′ N, Long 97° 55′ E; Fig. 1), is a 40,273 ha permanent U.S. Army Forces Command Reservation and is the site of ongoing military training. Training operations include field maneuvers, combat vehicle operations, mortar

and artillery fire, small arms fire, and aircraft flights (U.S. Army 1994). A 6480 ha Impact Area is off limits to maneuver training, public use, and most management activities at all times (Fig. 1). The Multipurpose Range Complex (MPRC) and the adjacent danger fan are closed to training and public use during live fire exercises. The remaining 4960 ha of training grounds that lie outside the MPRC and the danger fan are generally open throughout the year except during large scale training maneuvers held for several weeks in the spring and fall.

The Flint Hills extend from northeastern Kansas south to northeastern Oklahoma. Row crop agriculture is limited in the Flint Hills because of extensive limestone breaks and a shallow, rocky soil (Zimmerman 1985); most of the region is used as pasture. Landcover on Fort Riley includes native grassland and non-native planted grassland, open savannah, and wooded riparian lowlands (U.S. Army 1994). Pre-settlement grasslands in this region were comprised primarily of tallgrass prairie species interspersed in places with some mixed-grass prairie species (Kuchler 1974). Land uses and management prior to acquisition by the Army included agriculture, domestic livestock grazing, and fire suppression. Today, grasslands on Fort Riley experience varying levels of military disturbance. Mature riparian forest with shrubby edge occurs along lowland intermittent and perennial streams, and isolated patches of both trees and shrubs occur along intermittent drainages within the grasslands. Common woody species include rough-leaved dogwood (*Cornus drummondi*), plum (*Prunus americana*), smooth sumac (*Rhus glabra*), eastern red cedar (*Juniperus virginiana*), red mulberry (*Morus rubra*), osage orange (*Maclura pomifera*), and honey locust (*Gleditsia triancanthos*).

Management history.—Grazing is not permitted on Fort Riley; much of the area is hayed each year in conjunction with a hay lease program involving local landowners. Haying generally occurs in July on upland grassland sites that contain few trees and shrubs. Records are not kept as to which locations are hayed in a given year. Areas of the study site that were hayed during July 1995 and 1996 were recorded during this study.

Fort Riley's prescribed burn program operates from March through May (U.S. Army 1994). Approximately one-third of the Reservation is burned each year on a rotational basis, creating a planned burn interval of about three years for most areas. Training related wildfires occur throughout the year; consequently both the area burned and the frequency of burning in a given location can vary widely from year to year. The Fort Riley Natural Resources Office maintains records of all planned burns and most wildfires. This information was used to determine the burn history of the study area during the period 1992–1996.

Bird surveys.—In 1995, permanent bird survey points (n = 119) were located at approximately 500 m intervals along transects 5–7 km in length. All survey points were placed outside of areas of restricted access such as the MPRC and the danger fan. Each survey point was marked with flagged fence posts; Universal Transverse Mercator (UTM) coordinates were recorded using a Global Positioning System (GPS) unit.

From May–August, 1995, and from March–July, 1996, we made eight timed monthly surveys at each survey point using a modified variable circular-plot method (Reynolds et al. 1980) to locate breeding shrikes. The UTM coordinates of the specific location of each shrike use site was recorded. Each transect was surveyed beginning at first light and was completed by three hours after sunrise. Surveys were not conducted during heavy fog, rain, or when wind speeds exceeded 20 km/hr. In order to minimize sampling bias, the order in which transects were surveyed each month and the starting point and direction in which points were sampled along the transect were varied randomly. Because breeding shrikes were found to be relatively scarce on Fort Riley during the 1995 field season, in 1996 UTM coordinates were also recorded for birds found during the course of other field work. The date each bird was observed, the activity of the bird, and the type of perch being used (e.g., tree, shrub) when the bird was first located were recorded.

Landscape scale habitat.—For landscape scale analysis, the habitat within a 250 m radius of each survey point (a 19.6 ha plot) was identified, *a priori,* as either grassland (n = 35), savannah (n = 44), or woodland edge (n = 40) according to the amount of cover by woody vegetation. The habitat class for a point was determined using a tree cover map developed by Kansas Biological Survey (KBS; Lauver et al. 1996) and on-site visual estimations. Grassland plots contained 15 or fewer isolated shrubs (<4 m in height) or trees (>4 m in height) or one copse 20 m in diameter. Savannah plots contained more than 15 shrubs or trees and did not contain continuous, wooded riparian habitat. Woodland edge points were located within 100 m of extensive, wooded riparian habitat that ran through the plot. The landscape habitat category of specific shrike locations (use sites) was determined using the same methods as for the survey points.

Use sites and survey sites were grouped into five burn treatments, based on the year the site was last burned, and two hay treatments, based on whether or not the site was hayed in 1995. A χ^2 analysis was conducted to determine if the observed frequencies of shrike use sites differed from a random distribution among the three habitat types, among the burn treatments, and among the hay treatments.

Fine scale vegetative structure.—Fine scale vegetation was sampled at use sites and survey sites during the spring and summer of 1996. Using a table of random digits, sampling plots were permanently located at a random distance (within 200 m) and direction from each survey point. Vegetation sampling plots were also centered around use sites in order to describe shrike fine-scale habitat. The density of shrubs (<4 m in height) and trees (>4 m in height) was measured within the sampling plot. Four meters height was selected because that was the minimum height a tree

could be detected using the remote sensing techniques employed by KBS (Lauver et al. 1996).

A point-intercept method was developed (modified from Rotenberry and Wiens 1980) to sample the structure of the herbaceous vegetation at 100 randomly located sampling points within the plot. At each of the 100 points within the plot, a 6 mm diameter rod marked in 10 cm intervals was dropped vertically through the vegetation. At each sampling point, the number of contacts of vegetation within each decimeter of the sampling rod was recorded according to the physiognomic class of the vegetation (live grasses, live forbs, standing dead vegetation). These samples were used to calculate measures of herbaceous vegetative cover and vertical and horizontal vegetative structure. Percent cover by each physiognomic class present at a site was calculated from the frequency of occurrence of each class at all 100 sampling points. Total vegetative cover was estimated as the proportion of points with at least one of the physiognomic classes of vegetation. Percent cover of litter was calculated as the proportion of sampling points with litter. When litter was present, its depth (cm) was measured and recorded. The maximum height of the vegetation contacting the rod at each sampling point was also recorded. The vertical density of the vegetation was calculated as the mean number of contacts of vegetation with the sampling rod. Two heterogeneity measures were calculated. The first was the coefficient of variation of the maximum height of the vegetation across the sampling plot. The second was the coefficient of variation of the vertical density of the vegetation across the sampling plot. Physiognomic cover diversity was calculated after Wiens and Rotenberry (1981) using Hill's (1973) reciprocal of Simpson's (1949) diversity index as

$$P = 1/\Sigma\, p_i^2,$$

where P is the physiognomic cover diversity index, and p_i is the proportional coverage of the ith physiognomic class. This index indicates the equivalent to the number of physiognomic vegetation classes if all were equally abundant.

The severity of military disturbance to the vegetation was also identified at the fine scale. If vehicle tracks were intercepted by the sampling rod, the sampling point was given a score indicating the intensity of damage to the vegetation: 0 (no disturbance), 1 (crushed vegetation, little soil disturbance), 2 (extensive disruption of the soil, little remaining vegetation), or 3 (permanent gravel road). A military disturbance index was calculated for each site as the sum of the disturbance scores for all 100 sampling points within the plot.

Principal components analysis.—The spring 1996 fine-scale herbaceous vegetation data describing the bird survey points represent the range of values for the vegetative structure available to shrikes during the period of peak territory establishment (Tyler 1992). For this reason, these data were used as the baseline data for all comparisons. Because measures of vegetative structure are highly correlated with one another (James 1971, Wiens and Rotenberry 1981), a principal components analysis (PCA) was conducted on the spring data to identify the patterns of covariation among the herbaceous vegetation variables. Principal components analysis has the advantage of reducing a large number of covarying variables to a smaller number of orthogonal components that maximize the variance accounted for in the data (Rotenberry and Wiens 1980, Gauch 1982). Habitat data from the shrike use site were applied to the early or late spring principal components to ordinate shrike use sites in the principal component space defined by the census points. By plotting shrike use site vegetation data in the principal component space defined by the spring survey point vegetation data, comparisons of the principal component scores using analysis of variance (ANOVA) could be made between use sites and survey sites in order to detect patterns of bird-habitat associations. Spring vegetation was sampled in early April and late May because a reservation-wide training exercise restricted access to the study site during late April and early May. A series of ANOVAs conducted on the principal component scores for sites sampled before and after the start of the growing season showed significant changes in each of the principal components, indicating that the date the data were collected may influence comparisons of vegetative structure among treatment groups. For this reason, the spring 1996 sampling period was treated as two separate sampling periods (early and late), and the principal component scores were grouped accordingly for further analysis.

All variables expressed as percentages were transformed using the arcsine square root transformation (Zar 1984) prior to analysis. Data are presented as mean ($\bar{x}$) ± standard error (SE). Significance was established at $P = 0.05$ for all comparisons.

The Shapiro-Wilk test (SAS Inst., Inc. 1992) was used to test the univariate assumption that the data are normally distributed, and Levene's test was used to test the univariate assumption that the treatment group variances were equal. For those comparisons for which the treatment variances were unequal, the SATTERTH option within the PROC MIXED procedure in SAS (SAS Inst., Inc. 1992) was employed to calculate appropriate degrees of freedom and fit the unequal variance model. If the Satterthwaite method did not change the results of the ANOVA, the test was assumed to be robust despite the heterogeneous variances, and the original data were retained. If, by fitting the unequal variance model, the results of the ANOVA changed, the test was conducted using the new degrees of freedom. Statistical analyses were performed using SAS (Version 6.11) software on an IBM compatible computer.

RESULTS

Landscape scale.—Seven shrike use sites were located in 1995 and 12 use sites were located in 1996. All birds were observed dur-

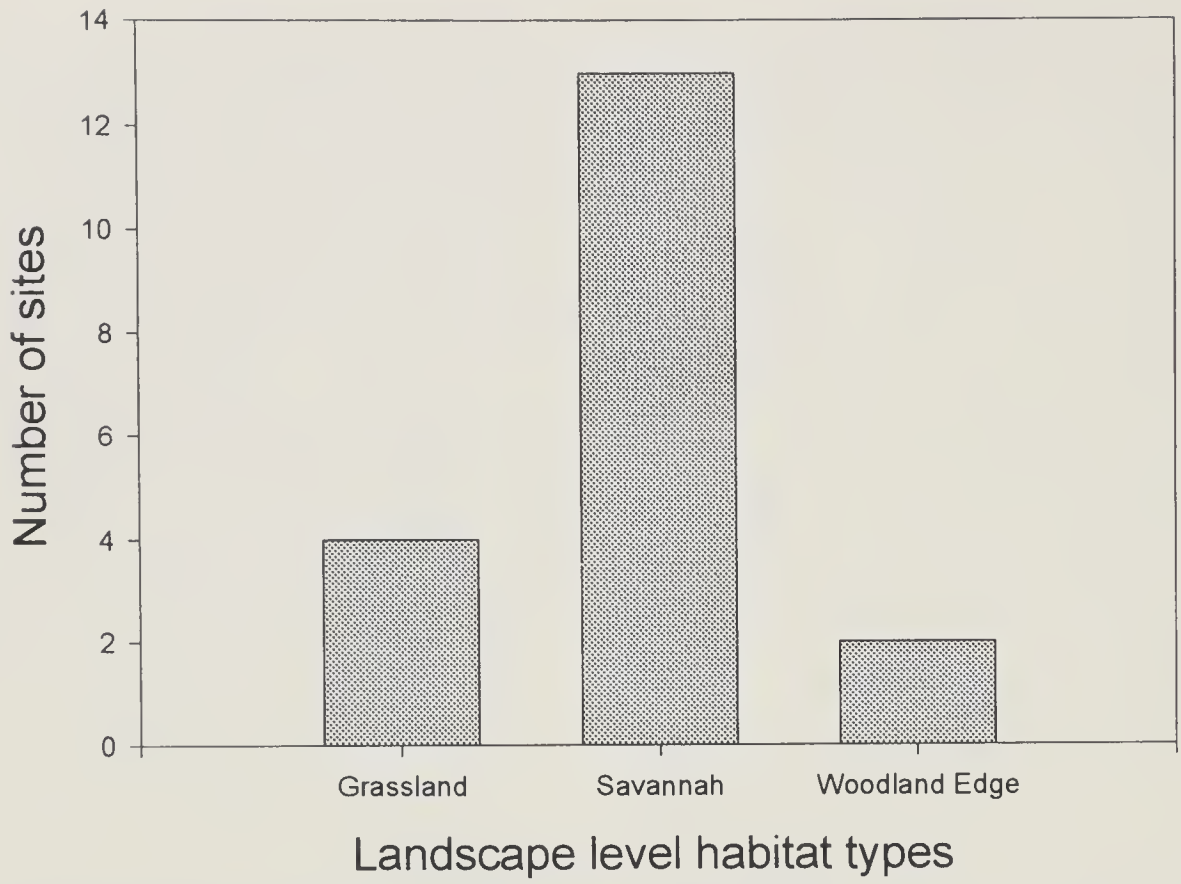

FIG. 2. Distribution of pooled 1995 and 1996 Loggerhead Shrike use sites (n = 19) among landscape level habitat types, fort Riley Military Reservation, Kansas (χ^2 = 10.17, 2 df, P = 0.0062).

ing the breeding season and were assumed to be independent breeding individuals based on territorial behavior and the large distance (usually >1 km) between locations. Six of seven shrike observations in 1995, and 4 of 12 in 1996 were made at survey points. In 1995, we observed shrikes twice at one point on different surveys (counted as one bird), and in 1996, two birds were seen twice at the same point (also each counted as one bird). We located nests for two of the sightings in 1995 and six in 1996; thus we documented breeding for 8 of 19 birds by locating nests. Shrikes were most often observed foraging (n = 14). Shrikes were significantly associated with savannah habitat at the landscape scale (χ^2 = 10.17, 2 df, P = 0.0062; Fig. 2).

Approximately 30% of the study area was hayed in 1995 (33 of 104 sites). In 1996, shrikes selected sites randomly with respect to hay treatment (n = 12, χ^2 = 0.05, 1 df, P > 0.05). Four of the seven Loggerhead Shrike use sites located in 1995 were at sites burned two years earlier (in 1993). The other three use sites located in 1995 were burned three years before (in 1992). The majority of shrikes located in 1996 (n = 12) selected sites that were either burned in 1996 (n = 5) or last burned in 1993 (n = 5). This distribution was not significantly different from random with respect to the number of years since the site was last burned (χ^2 = 4.45, 4 df, P > 0.05).

Fine scale.—In 1996, vegetation sampling plots were centered on 12 Loggerhead Shrike use sites. Ten of the 12 sites were located and sampled during the early part of the spring sampling period and were therefore compared to early spring survey sites sampled before the middle of May (n = 54).

The PCA of the spring 1996 fine-scale herbaceous vegetation data resulted in three principal components with eigenvalues greater than one (Table 1). Together, these components accounted for 84.0% of the total variance present in the data. High values of the first principal component (PC1) represent increasing total vegetative cover and vertical density, increasing cover by litter, and decreasing heterogeneity. High values of PC1 are representative of undisturbed tallgrass prairie, whereas low values of PC1 indicate high vertical and horizontal heterogeneity.

TABLE 1. Eigenvectors of fine scale vegetative variables for the first three principal components determined by a PCA of spring 1996 bird survey site herbaceous vegetation data. Values next to the habitat variables under PC1, PC2, and PC3 are factor loadings. Only loadings with values > |0.30| are included.

Variable	PC1	PC2	PC3
Eigenvalue	6.11	3.15	1.66
Variance explained	47%	24%	13%
Cumulative variance	47%	71%	84%
Cover			
Vegetation cover	0.393		
Standing dead cover		0.374	
Live grass cover		−0.358	
Live forb cover		−0.336	
Litter cover	0.302		
Physiognomic diversity			0.633
Vertical structure			
Litter depth		0.454	
Contacts in first decimeter		−0.401	
Total hits	0.381		
Maximum vegetation height		0.330	
Heterogeneity indices			
Horizontal heterogeneity	−0.379		
Vertical heterogeneity	−0.359		
Military disturbance			0.588

High values of the second principal component (PC2) represent increasing cover of standing dead vegetation, increasing maximum height of vegetation, increasing litter depth, and decreasing cover of live grass and live forbs, especially within 10 cm of the ground. Sites scoring highest on PC2 were those that had not been burned for three or more years, whereas sites with low PC2 scores generally were sites burned in 1996. High values of the third principal component (PC3) represent increasing physiognomic coverage diversity and increasing severity of military disturbance.

There was no significant difference at the fine-scale in the density of shrubs (F = 3.65, 1, 63 df, $P > 0.05$) or trees (F = 0.68, 1, 63 df, $P > 0.05$) among shrike use sites and survey sites (Table 2). The mean value of PC1 (vegetative cover and density, litter cover, and structural homogeneity) for shrike use sites was significantly lower than the mean value of PC1 for survey sites (F = 7.43, 1, 63 df, $P = 0.0083$), indicating selection of habitat with above average horizontal and vertical heterogeneity.

Levene's test was significant for heterogeneous variances of PC2 scores between shrike use sites and survey sites ($P = 0.0439$). When the appropriate degrees of freedom were estimated (SATTERTH; SAS Inst., Inc. 1992), the initial results of the ANOVA changed, so the Satterthwaite estimates were retained (Table 2). Mean PC2 scores (litter depth, and height and cover by standing dead vegetation) for shrike use sites were significantly higher than those for the survey sites (Table 2). Mean PC3 scores (physiognomic cover diversity and disturbance index) did not differ between shrike use sites and survey sites (F = 0.14, 1, 65 df, $P > 0.05$; Table 2).

Military track disturbance.—No significant differences existed between Loggerhead Shrike use sites and survey sites with regard to military disturbance (F = 2.06, 1, 63 df, $P > 0.05$). The statistical power of this test was low (0.35) however, meaning that the failure to reject the null hypothesis when the alternative hypothesis is true is expected to occur with a 65% probability (Dallal 1988). This

TABLE 2. Loggerhead shrike use site means and site F-test *P*-values for early spring 1996 fine scale vegetative variables measured at Fort Riley Military Reservation, Kansas.

Vegetative variable	Early spring survey sites (n = 54)	Loggerhead Shrike use sites (n = 10)	*P*-value
Number of shrubs	10.98 ± 2.25	20.92 ± 4.69	>0.05
Number of trees	6.92 ± 1.61	10.00 ± 3.36	>0.05
Principal component 1	−1.37 ± 0.34	−3.52 ± 0.71	0.0083
Principal component 2	0.73 ± 0.28[a]	2.19 ± 0.29[a]	0.0010[b]
Principal component 3	0.12 ± 0.19	0.28 ± 0.40	>0.05

[a] Unequal variance estimates.
[b] *P*-value is the result of using unequal variance estimates. Difference of LS Means = −1.46, and SE of the difference = 0.40.

means that it is inappropriate to use these results to argue that disturbance does not affect Loggerhead Shrikes. We merely have not shown that disturbance does affect them. This means that shrike use sites are typical, with respect to disturbance, of the rest of the grassland that we surveyed. The average survey point had a disturbance score of 35 (±28.7 SD, range 0–204), similar to our disturbance scores for the sites used by shrikes.

DISCUSSION

The scale at which an ecological study is conducted is an important factor in the interpretation and understanding of the patterns observed (Forman 1995, Wiens et al. 1987, Wiens 1989). For example, the presence of several shrubsteppe bird species have been correlated with different vegetative characteristics at the regional and local scales of study (Wiens et al. 1987). We investigated Loggerhead Shrike habitat associations at both a landscape scale defined by macrohabitat types and at a finer scale within individual territories. Analysis at these two scales resulted in different patterns of woody vegetation associated with breeding locations used by shrikes.

At the landscape scale, shrikes at Fort Riley were associated with savannah habitat, suggesting that at this scale shrikes selcct sites in the tallgrass prairie with scattered woody vegetation. This pattern of selection is similar to that found for shrikes elsewhere in the United States. It supports the hypothesis that the availability of nesting sites is an important factor in habitat selection by breeding shrikes (Brooks and Temple 1990, Yosef and Grubb 1994).

At the fine-scale, shrike habitat at Fort Riley did not differ in either mean shrub density or mean tree density from random survey sites. Since the majority of the birds (70%) observed at use sites were foraging, these results suggest that the density of woody vegetation at the finer scale may be unimportant to foraging Loggerhead Shrikes. While the majority of shrikes in this study were first seen perched on woody vegetation, this may be because they are more easily seen perched at these heights. During further observation, birds were often seen perched on prairie grasses and forbs ranging in height from 0.5–2 m. In contrast to homogeneous pastureland, the structural heterogeneity of tallgrass prairie provides shrikes with perching and foraging substrates other than offered by woody vegetation (Chavez-Ramirez et al. 1994).

The importance of vegetative structural heterogeneity to shrikes is shown by the fact that shrikes used sites at Fort Riley that had significantly greater structural heterogeneity (low values of PC1) than did random sites. Shrikes also used sites with lower total vegetative cover, lower litter cover, and more bare ground (low values of PC1); taller vegetation, standing dead vegetation, and deeper litter (high values of PC2) than random sites. These results suggest that structurally heterogeneous native prairie that has tall vegetation interspersed with areas of bare ground may provide shrikes with adequate foraging habitat at the fine-scale.

Shrikes used sites with high structural heterogeneity despite the fact that they did not differ from random with respect to burn history, haying the year before, or the military vehicle track disturbance index. We predicted that shrikes would be associated with high vegetative structural heterogeneity, and that the heterogeneity would be associated with greater military vehicle track disturbance. It is reasonable to expect that even moderate levels of military vehicle track disturbance to the vegetation are capable of creating the structurally heterogeneous ground cover selected by shrikes at Fort Riley.

It is possible that vehicular disturbance to the vegetation may help sustain scattered woody vegetation at the landscape scale for breeding shrikes. Military vehicle activity, crushing vegetation, creating bare patches, and soil compaction, may have indirect effects on the vegetation at Fort Riley because of interactions with hay harvest and fire. For example, at Konza Prairie Research Natural Area, a Long Term Ecological Research site, annual and 2-yr burn intervals in watersheds without vehicle track disturbance eliminate woody vegetation and most forbs, yielding a structurally simple plant cover of mostly warm-season grasses without vertical and horizontal habitat variability like that at Fort Riley. Despite the burning of most areas of Fort Riley every 2–4 years, many scattered, isolated trees and hedgerows exist at the landscape scale and represent potential nesting

habitat for Loggerhead Shrikes (Lauver et al. 1996). By fragmenting patches of herbaceous vegetation and reducing soil drainage through compacting, vehicular disturbance may indirectly reduce the intensity of fire in localized areas, thus reducing the fire-caused destruction of established woody vegetation.

The results from this study show that shrikes at Fort Riley are associated with scattered trees and shrubs at the landscape scale and with structurally heterogeneous herbaceous vegetation at the fine-scale. Military training may have both short and long term roles in maintaining shrike habitat at both scales. In order to better understand the relationship between training and habitat conditions, the long term effects of training disturbance to shrike habitat at Fort Riley need to be studied.

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FOOD OF NESTLING NORTHWESTERN CROWS

N. A. M. VERBEEK

ABSTRACT.—Northwestern Crows (*Corvus caurinus*) are typically associated with intertidal beaches where they search for food. In this study I examined the diet fed to nestling crows to determine the importance of intertidal beaches as a food source on Mitlenatch Island, B.C. The diet consisted of marine and terrestrial invertebrates and vertebrates, and fruit. Lepidoptera, Mollusca, Crustacea and Pisces were the most important taxa in terms of total dry weight fed to nestlings. During low tide, when crows have a choice of feeding intertidally or on land, 67% of the diet in terms of dry weight came from terrestrial sources. *Received 15 Oct. 1997, accepted 30 July 1998.*

Northwestern Crows (*Corvus caurinus*) typically occur near tidal shores along the coast of northwestern North America (Godfrey 1966). Like other species in the genus (Kalmbach 1939; Lockie 1955, 1956; Tenovuo 1963; Houston 1977; Hogstedt 1980), adult Northwestern Crows eat a variety of food (Butler 1974). Northwestern Crows feed in the intertidal zone during low tides, eat stored food, or search other habitats during high tides (Butler 1974, 1980; James and Verbeek 1983). Butler (1980) reported on the diet fed to the young in four nests near intertidal beaches. The objectives of this study were to determine the diet of nestling Northwestern Crows on Mitlenatch Island from a larger sample of nests located throughout the island than was available to Butler (1980), and to what extent nestling diet depends on intertidal, marine food.

STUDY AREA AND METHODS

Northwestern Crows were studied on Mitlenatch Island, Strait of Georgia, British Columbia, from 14 May–3 July 1983. The vegetation on the island consisted of patches of shrubs and trees interspersed with meadows (Brooke et al. 1983). Two extensive intertidal beaches provided access to marine invertebrates. The island was used as a nesting site by several marine birds, with the eggs, chicks and fish dropped by Glaucous-winged Gulls (*Larus glaucescens*, 2100 pairs; Campbell et al. 1990) and Pelagic Cormorants (*Phalacrocorax pelagicus*, 315 pairs; Campbell 1990) serving as important food sources for the crows. Nestling food was obtained by encircling the necks of each nestling in a nest with a loop of pipe cleaner to prevent them from swallowing the items. The pipe cleaners were left on for 45 min. This method had no apparent detrimental effect on the nestlings. Fledging success (% fledged of eggs hatched) of collared young in this study was 59%, compared to 37–67% reported earlier (Richardson et al. 1985). I returned to the nest after the parents had made 1–4 (exact number unknown, but see Butler 1980, James and Verbeek 1984) food deliveries to the young. I collected the food from all the young in a nest at that time, put it in a vial with 70% alcohol and treated it as one sample. In total, 388 samples were collected from 58 young in 22 nests located throughout the island, representing about a third of the crow nests on the island. For each food sample I noted whether the intertidal areas around the island were available to the crows (low tide, 279 samples) or not (109 samples). The samples were collected throughout the day, but as low tides in Georgia Strait tend to occur during the day in summer, low-tide samples predominated. Following identification, specimens belonging to the same taxon were lumped together, oven dried for 48 h at 70° C, and weighed. The average age of the young was 13.7 d (SD = 5.0, range 2–26, n = 388).

RESULTS

Marine food.—Polychaete worms were represented mostly by short pieces; the remainder of the worms having been left behind in the tubes among the intertidal boulders. Small decapods (ca 1.5 cm) were fed whole but larger ones were dismembered and legs and body parts fed as separate items. Intertidal Isopoda, represented by the genus *Ligia*, were fed whole. Among the Mollusca, chitons (Amphineura) were fed whole, but clams (Pelecipoda) were removed from the shell and fed in pieces. Fish (species not identified) were found in many samples. The crows caught some stranded fish in tide pools or when they were uncovered hiding among marine algae at or near the tide line. These fish were fed whole when small or in pieces when large. At least 90% of the fish flesh, based on my experience of 7 years of daily visits to about 300 gull nests (Verbeek, 1984, 1986, 1988) and countless hours of watching crows feeding in

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the interidal (Verbeek 1998), was regurgitated by the gulls in the colony. It was recognizable as regurgitated fish because the flesh had mostly disintegrated following partial digestion by the gulls.

Terrestrial food.—Most terrestrial food consisted of invertebrates with some families important in number (Table 1). Terrestrial Isopoda (sow bugs) were represented by the genus *Porcelio*. The smallest invertebrates taken were froghoppers (Cercopidae, Homoptera), some as small as 4 mm. Among moths (Lepidoptera), lasiocampids (tent caterpillars) and tortricids (leaf rollers) predominated. Lasiocampids occurred mainly as pupae (97.7%, the remainder being adults) found among ground vegetation, while the tortricids were mainly larvae (96.9%). Craneflies (Tipulidae, Diptera) were represented as adults. One food sample contained 200 similar cycloraphid (Diptera) pupae that I could not identify to family, hence the large number of unknowns. Most Hymenoptera were carpenter ants (*Camponotus* sp., Formicidae) caught in the air during their nuptial flights, found dead on the tide line, or found alive on land. Many spiders (Araneida) were taken, particularly three families (crab spiders, Thomisidae and Philodromidae; and jumping spiders, Salticidae). These are generally mobile, grassland species that pursue their prey and thus draw attention to themselves. The crows also took many harvestmen (Phalangida), some with bodies as small as 4 mm.

Vertebrates fed to nestlings other than fish regurgitated by gulls, included pieces of coast garter snake (*Thamnophis elegans*). The longest snake I saw killed by crows was 79 cm. I also found the front half of a pacific treefrog (*Hyla regilla*), pieces of deer mouse (*Peromyscus maniculatus*), a piece of a nestling Song Sparrow (*Melospiza melodia*), and pieces of what I presumed were gull embryos and chicks. Fruits fed to the young consisted of 3 western service berries (*Amelanchier alnifolia*) and 50 trailing blackberries (*Rubus ursinus*). Only one food sample contained a piece of grit.

Relative importance of taxa.—Lepidoptera, Diptera and Araneida predominated in terms of total numbers encountered in the food samples (Table 2). Because several taxa (Decapoda, Mollusca, Pisces, Aves) in Table 2 are represented by pieces, rather than whole animals, I could not present the data in terms of percentage composition by number of individuals. In terms of percent occurrence, seven taxa were represented in more than 25% of the samples. This included the three taxa mentioned, Coleoptera, and three marine taxa, Mollusca, Crustacea, and Pisces. Analysis by dry weight showed that the bulk of the diet consisted of Lepidoptera (mostly *Malacosoma* spp.), Mollusca (mostly bivalves), Pisces, and Crustacea (mostly crabs, Table 2).

Source of food.—Although Northwestern Crows feed intertidally when possible (Butler 1974, 1980; Richardson 1983; James and Verbeek 1983), they took fewer (n = 399) intertidal organisms (fish excluded) to their nestlings than terrestrial items (n = 2723, fish excluded) during low tide. In terms of total dry weight (fish included, assuming that 90% of the fish fed during low tide came from the bird colonies), 67% (74.8 g dry weight) of the nestling diet came from terrestrial sources and 33% (36.8 g) from the intertidal during low tides. The number of samples with or without fish did not differ significantly between low tide (83 samples with, 196 without) and high tide (29, 80, respectively; G test: G = 0.178, $P > 0.05$). Fish was available to the crows at all times, regardless of the tides, because most fish was obtained in the gull colony. As expected, significantly (G test: G = 16.74, $P < 0.001$) more samples contained intertidal food other than fish during low tide (140 samples with, 139 without) than during high tide (30, 79, respectively). Thus, marine food other than fish continued to be fed to the nestlings even during high tide.

DISCUSSION

The nestling diet is diverse and includes both terrestrial and marine organisms (Table 1). The pipe cleaner method I used to obtain food samples has one drawback in that it does not catch soft material, such as egg yolk (Butler 1974, 1980). On the other hand, even tiny, soft-bodied insects are readily trapped in the tangle of legs of larger insects and saliva. Although marine organisms (fish excluded) are available to the crows only during low tide, some of them are cached (Butler 1980, Verbeek 1997), particularly clams (James and Verbeek 1983). Subsequent retrieval of cached items enables crows to continue to feed ma-

TABLE 1. Number of food items (n = 4877) belonging to various taxa, in the nestling diet of Northwestern Crows on Mitlenatch Island, B.C.

Taxon	n
Fruit	53
Annelida (worms)	20
Crustacea (crabs, etc.)	
Decapoda	234
Isopoda	64
Amphipoda	20
Myriapoda (centipedes, etc.)	
Diplopoda	5
Chilopoda	1
Insects	
Orthoptera (grasshoppers)	
Acrididae	56
Trichoptera (caddisflies)	
Limnephilidae	1
Dermaptera (earwigs)	
Labiduridae	21
Forficulidae	15
Unknown	1
Mallophaga (feather lice)	3
Hemiptera (bugs)	
Scutelleridae	106
Corizidae	10
Pyrrhocoridae	5
Pentatomidae	5
Saldidae	2
Unknown	6
Homoptera (leafhoppers)	
Cercopidae	245
Cicadellidae	11
Aphididae	5
Unknown	1
Coleoptera (beetles)	
Elateridae	100
Cleridae	25
Curculionidae	22
Carabidae	13
Scarabaeidae	12
Dytiscidae	7
Unknown	10
Lepidoptera (moths, etc.)	
Lasiocampidae	715
Tortricidae	430
Noctuidae	99
Geometridae	17
Gracilariidae	17
Pyralidae	7
Unknown	23
Diptera (flies)	
Tipulidae	377
Culicidae	111
Otitidae	62
Chironomidae	50
Bibionidae	26
Heleomyzidae	31
Dolichopodidae	12
Empididae	8
Anisopodidae	6
Tachinidae	4
Syrphidae	3
Coelopidae	3
Anthomyiidae	2
Dryomyzidae	2
Muscidae	2
Tabanidae	2
Unknown	260
Hymenoptera (ants, wasps, etc.)	
Formicidae	198
Andrenidae	32
Ichneumonidae	13
Tenthredinidae	10
Tiphiidae	2
Vespidae	1
Araneida (spiders)	
Thomisidae	239
Philodromidae	223
Salticidae	185
Clubionidae	41
Lycosidae	36
Anyphaenidae	7
Gnaphosidae	7
Tetragnathidae	7
Araneidae	6
Theridiidae	3
Unknown	21
Phalangida (harvestmen)	207
Mollusca (molluscs)	
Pelecypoda	125
Gasteropoda	15
Amphineura	8
Echinodermata (seastars, etc.)	1
Vertebrates	
Pisces	96
Aves	25
Reptilia	13
Mammalia	7
Amphibia	1

TABLE 2. Total number (n = 4877) of food items found in the diet of Northwestern Crow nestlings on Mitlenatch Island, B.C. and number of samples (n = 388) in which they occurred, and total dry weight.

Taxon	Number encountered	Number of samples[a] in which they occurred		Dry weight (g)	
		n	%	Total	%
Fruit	53	33	8.5	5.16	3.2
Annelida	20	19	4.9	3.32	2.1
Crustacea	318	106	27.3	21.84	13.7
Myriapoda	6	3	0.8	0.04	trace
Orthoptera	56	45	11.6	0.78	0.5
Trichoptera	1	1	0.2	trace	trace
Dermaptera	37	21	5.4	0.90	0.6
Mallophaga	3	3	0.8	trace	trace
Hemiptera	134	56	14.4	1.40	0.9
Homoptera	262	60	15.5	0.52	0.3
Coleoptera	189	99	26.4	2.36	1.5
Lepidoptera	1308	196	50.5	50.07	31.4
Diptera	961	136	35.1	4.97	3.1
Hymenoptera	256	68	17.5	5.68	3.6
Araneida	775	181	46.6	4.81	3.0
Phalangida	207	64	16.5	0.51	0.3
Mollusca	148	99	25.5	22.51	14.1
Echinodermata	1	1	0.3	0.63	0.4
Pisces	96	111	28.6	25.91	16.2
Other Vertebrata	46	21	5.4	8.25	15.2

[a] Sample as defined in Methods.

rine food to their young during high tide. Northwestern Crows obtain some terrestrial food in shrubs and trees, but most food is found on the ground. Lepidoptera, mostly pupae of *Malacosoma* sp., were the most numerous, representing more than 35% of total dry weight (Table 2). The crows probably avoided *Malacosoma* caterpillars because they were hairy; they did eat noctuid, geometrid and tortricid caterpillars, all of which were non-hairy. In other dietary studies of nestling *Corvus* (Lockie 1956, Yom-Tov 1975, Houston 1977), earthworms (Lumbricidae) formed part of the diet. Mitlenatch Island has no earthworms, hence their absence in the diet. In Vancouver, B.C., adult Northwestern Crows do eat earthworms (pers. obs.). In contrast to Carrion Crows (*Corvus corone*; Yom-Tov 1975), Northwestern Crows took only adult craneflies. The pacific treefrog in the diet was unexpected as no amphibians occurred on the island. The frog was most likely caught on nearby (ca 6 km) Hernando Island, to which crows flew regularly. Nesting passerines are uncommon on the island (Verbeek, 1998), which explains why I found only one nestling in the diet.

Mitlenatch Island provides three sources of food for crows: intertidal areas; meadows, shrubs, and trees; and the colonies of nesting seabirds. The crows regularly fed among nesting seabirds, where they obtained regurgitated food (mostly fish), eggs, and chicks (Butler 1980, Verbeek 1982, Butler et al. 1984, Verbeek 1988). Dead gull and cormorant chicks and regurgitated fish attracted invertebrates to the seabird colonies, and crows likely took some of these as well, but I do not know how many or which ones. Some fish was also obtained intertidally (e.g., *Clinocottus acuticeps, Liparis florae, Anoplarchus purpurescens*; Butler 1980). Terrestrial invertebrates came from areas other than the seabird colonies as well. Thus, it is not possible to apportion much of the food fed to the nestlings during low tide to any one of the three specific sources. Considering only items in food samples fed during low tide, when the crows had a choice of feeding intertidally or elsewhere, marine food (intertidal invertebrates and fish, and all pelagic fish caught by the gulls) comprised 51% of total dry weight, and terrestrial invertebrates, vertebrates (minus fish), and fruit 49%, or 1132 and 1211 kJ, respectively,

using caloric values in Cummins and Wuycheck (1971), and Johnson and coworkers (1985). If I subtract 90% of the fish from the marine food and add it to the terrestrial food, then intertidal food represented 33% of total dry weight (704 kJ), versus 67% for food derived from all terrestrial sources (1693 kJ). Intertidal beaches are thus less important as a food source for nestling crows during low tide on Mitlenatch Island than I had expected. This does not mean that the intertidal beaches are unimportant to Northwestern Crows. As stated elsewhere (Butler 1980, James and Verbeek 1984), the intertidal areas are particularly important early in the nesting season. As the season progresses, the crows gradually de-emphasize their use of beaches in favor of grasslands as more and more invertebrates become available on land (Butler 1980). By the time the grasslands begin to dry out in early June and invertebrate abundance declines, the crows begin to spend more time in the bird colonies. Although there is an obvious influx in the tidal component of the diet during low tide, adults may find it energetically worthwhile to take abundant terrestrial food near the nest, regardless of the state of the tides. By foraging near the nest they may save time and energy otherwise expended in flight to more distant tidal sources and they can stay closer to the nest to protect its contents (Butler 1980). This is particularly important because the mean internest distance of the crows is small (Butler et al. 1984).

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ADVANTAGES OF COLONIALITY IN FEMALE BOAT-TAILED GRACKLES

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ABSTRACT.—In a South Carolina cattail marsh, female Boat-tailed Grackles (*Quiscalus major*) concentrated to nest on predator-safe islands patrolled by American alligators (*Alligator mississippiensis*). I examined several hypotheses regarding colonial nesting behavior of Boat-tailed Grackles. (1) I reject the null hypothesis that colony-nesting and solitary females do not differ in reproductive success. Solitary-nesting females had lower reproductive success (37%) than colony females (63%), a difference perhaps attributable to males' defense of colonies from predatory birds. (2) I reject the hypothesis that the physical characteristics of sites used for colonies differ from those that are not used. Islands occupied by colonies were the same as unoccupied islands in measurements of water depth and vegetation structure. Colony site use is therefore not a result of habitat heterogeneity. (3) I reject the hypothesis that breeding success does not differ between contemporaneous colonies. In two of four years, I found significant variation among colonies in percentage of nests that produced young. Nesting success was independent of colony size. (4) I accept the hypothesis that the reproductive success of colonial females is related to extrinsic factors rather than to differences in female quality. Predation was the main cause of nest mortality, and varied between colony sites, but its intensity was not related to colony size. Although clutch size remained constant over the nesting period, number of fledglings per nest decreased, mainly as a result of the increased proportions of nests lost to predators. Starvation, the second most important cause of mortality, did not vary according to colony size nor to time of breeding. Early synchronized nesting of the whole population may reduce the effects of predation by both a "head-start" effect, and by predator satiation.
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The number of mates that a male can monopolize depends on the spatial and temporal distribution of females (Emlen and Oring 1977), and on the male's competitive abilities (resource-holding potential of Parker 1974). Polygyny often occurs in colonial, non-territorial populations (Lack 1968) in which males have little influence on female distribution, and male-male competition limits access to females (harem polygyny of Wittenberger 1979). Harem polygyny has been found in many mammals, but rarely in birds (Emlen and Oring 1977, Wittenberger 1979). Among birds, it has been described for populations of large, sexually dimorphic oropendolas and grackles (Icteridae; Chapman 1929, Schäfer 1957, Tashian 1957, Drury 1962, Post 1992, Webster 1994). An understanding of how this mating system is maintained may be gained by considering the behavior of males and females separately, as each sex appears to act independently of the other until females actually choose colony sites.

Nesting female Boat-tailed Grackles (*Quiscalus major*) in South Carolina congregate in predator-secure sites, such as marsh islands patrolled by American alligators (*Alligator mississippiensis*; Post and Seals 1991, Post et al. 1996). Females build nests and rear young unaided by males. Males, which are 1.9× heavier than females, defend colonies from predatory birds. Females settle in colonies independently of male activities, but males adjust their behavior to maximize closeness to females. In each colony, an alpha male defends most receptive females from other males, and the clustering of females allows these males extreme reproductive advantage (Post 1992). Although the aggregation of females is advantageous to some males and may thus promote polygyny, the question of why females group in the first place should be addressed (Campagna et al. 1992). To examine this question, I consider the following hypotheses: (1) females nesting in colonies do not differ in reproductive success from females nesting alone; (2) the physical characteristics of sites used for colonies differ from those that are not used; therefore, aggregations may simply be a response to habitat heterogeneity; (3) as a corollary, if colony sites vary in quality, breeding success should vary between contemporaneous colony sites; (4) further, reproductive success should be related to extrinsic factors such as accessibility to predators,

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rather than to characteristics related to female quality, such as ability to gather food for young.

STUDY AREA AND METHODS

The study was conducted in a 30-ha impounded cattail (*Typha* spp.) marsh at Magnolia Gardens on the Ashley River 10 km north of Charleston, South Carolina. The outer part of the marsh was surrounded by a channel up to 3 m deep. Away from the channel, water depth in open water areas averaged 1 m. In 1985 open water covered 75% of the site and cattails covered 25%. Further descriptions of the study area are in Post and Seals (1991) and Post (1992).

Most nests were found during construction or egg-laying. I determined the date of clutch initiation of other nests by extrapolating from either date of hatching (one egg is laid each day; incubation, which begins with the penultimate egg, lasts 13 days), or from age of nestlings, determined by criteria in Bancroft (1984).

Nests were usually visited every three days. Estimates of nest survival probabilities are based on the time that nests were exposed to risk (Mayfield 1975, Johnson 1979). Only nests whose fates were known were included in the statistical analysis. The incubation period (13 days) and nestling period (13 days) were analyzed separately. To test for differences in nest success between solitary nests and colonial nests, I calculated the variance of the daily survival rate using the formula of Johnson (1979) and Hensler (1985). The Z-statistic was then used to test for differences between nesting success estimates (Hensler 1985).

Sources of mortality to nests were determined by examining the condition of depredated nests and their contents (Bancroft 1986). For example, a nest destroyed at night was assumed to have been taken by a snake or rodent. If the nest was disheveled and egg shell pieces were found, I inferred rodent predation. If the nest was intact and all signs of contents missing, I inferred snake predation. Daytime nest searches revealed the presence of snakes, which often rested in nests. Rodents left the marsh during the day, but fresh feces could be found in depredated nests. Starvation was inferred from the condition of a nestling; e.g., it was often listless, and showed little apparent weight gain in comparison to nestmates. Dead nestlings under six days old were removed by the females; older ones were left in the nest. Partial losses of nest contents to avian diurnal predators was possible, but smaller predatory birds (e.g., Blue Jays; *Cyanocitta cristata*), were not seen in the study area and large birds such as Fish Crows (*Corvus ossifragus*) would have taken the entire contents of nests (pers.obs.).

To address the question of whether areas used for nesting colonies differed from those not used, I followed these procedures: during 10–16 April 1992, I chose 10 islands, 5 of which had colonies with more than 10 nests and 5 which had no nests, but which had been used as colony sites in the previous year. At the end of the nesting season (July) I confirmed that no female grackles had nested in the latter sites. The islands all were about the same size (300 m^2) and were the same distance from the upland edge of the marsh and from open water. I placed ten 1-m quadrats in each site along a transect through the long axis of the island. I positioned the quadrat by throwing a meter-stick over my back and then putting the quadrat over the center of the point where the stick fell. After taking three paces, I repeated the procedure. I made four measurements: water depth, maximum height of vegetation, number of residual (overwintering) cattail stems per m^2, number of green cattail stems per m^2.

To determine whether females followed each other in and out of colonies, I used observation points from which I could see females approaching or leaving each colony for at least 100 m in any direction. A female was classified as being followed if, during the period it was in view within the 100-m radius, another female from its colony used the same flight path.

To gather information about food that females brought to nests in April–May of 1985–1986, I placed pipe cleaner ligatures (Orians 1966) around the necks of all nestlings in a series of randomly chosen nests. After 0.5 h, I retrieved all food from nestlings' throats and from the nest cup, and removed the pipe cleaners. Each nest was sampled once.

Females nested in groups of 2–37 (Post 1974). For purposes of analysis, groups of five or more simultaneously active nests, with no nest farther than 12.5 m from any other, were classified as colonies. Solitary females nested more than 25 m from any other female.

RESULTS

Breeding success of solitary vs colonial females.—Each year a small percentage of females nested outside colonies. Isolated females nested on cattail islands similar to those occupied by colonies, but nested more than 25 m from other females. I studied 58 solitary nests over five years (1986–1990). I detected significant differences in the daily nest survival rates between isolated and colonial females in two years: daily nest survival during the nestling stage was significantly lower for isolated females in 1988 ($Z = 2.21$, $P < 0.05$, $n = 19$ nests in each group) and 1989 ($Z = 1.76$, $P < 0.05$, $n = 12$). Differences in nesting success were due to predation, which accounted for 46% of mortality to eggs or nestlings of solitary females, versus 32% for progeny of colony females, a significant difference ($\chi^2 = 8.5$, $P < 0.01$, df = 1).

Colony site characteristics.—Most nests (96% of 1354) were in colonies (groups of five or more nests) on small cattail islands or narrow peninsulas in open water occupied by

TABLE 1. Nest survival rates of lone and colonial females.

		Percentage of nests surviving during:					
		Egg period (13 d)		Nestling period (13 d)		Total period (26 d)	
Year	n[a]	Lone	Colony	Lone	Colony	Lone	Colony
1986	8	64.4	72.0	58.8	85.1	37.7	61.3
1987	11	51.9	79.0	100.0	100.0	51.9	79.0
1988	19	51.1	77.9	36.4[b]	81.7	18.6	50.3
1989	12	49.9	45.5	64.4	100.0	32.1	45.5
1990	8	52.2	100.0	82.7	76.5	43.2	76.5

[a] The number of nests in each category.
[b] Daily nest survival significantly higher for colony nests (1988: $Z = 2.21$; $P = 0.014$; 1989: $Z = 1.76$; $P = 0.039$).

alligators. The mean area of 10 colony sites was 310.4 ± (SD) 144.8 m^2.

Many apparently suitable colony sites were not occupied. The non-colony islands were about the same size as colony islands and equidistant from the edge of the marsh (figure in Post 1992). For the characteristics that I measured, colony sites did not differ significantly from unoccupied islands [water depth: colony: 24.5 ± 1.5 cm, unoccupied: 28.3 ± 1.5 cm, $t = 1.8$, $P > 0.05$; vegetation height: colony: 153.2 ± 3.2 cm, unoccupied: 148.2 ± 2.9 cm, $t = 1.1$, $P > 0.05$; vegetation density (stems/m^2): colony: 30.2 ± 1.2, unoccupied: 31.9 ± 1.1, $t = 1.0$, $P > 0.05$; ratio of residual to green vegetation: colony: 1.10 ± 0.06, unoccupied: 0.98 ± 0.05, $t = 1.6$, $P > 0.05$; $n = 50$ for each site category for each measure].

Reproductive success and sources of mortality in different colonies.—Although areas used for colonies did not appear to differ from each other physically, nest success (percentage of nests producing at least one fledgling) differed between colony sites. The mean annual difference between the most successful and least successful colony over six years was 49.2%. In three of the six years, I found significant overall variation in success between colony sites (Table 2).

Most mortality to nest contents was from predation (33.6% of 2202 destroyed eggs or young; Table 3). Next in importance was starvation (26.4%), followed by nest abandonment (14.1%), hatching failure (9.4%) and collapse of nest support (7.7%; Table 3). Nest abandonment and collapse of nest were partly related to predator activity; some females deserted nests when snakes moved into a colony, and some nests were knocked down by alligators climbing into colonies to bask. Not all colonies were found by snakes, which contributed to significant variation in colony success (Table 2). For example, the years with lowest nesting success, 1985 and 1989, had the highest mortality from predation. In these years water levels were low enough to expose mudflats over which snakes could move into colonies. The low success of nests in 1988 was related to both predation and starvation, mortality factors which are not independent, as females may desert nests with young when colonies are invaded by snakes. Male grackles invariably attacked predatory birds near colonies and females occasionally joined in mob-

TABLE 2. Variation in reproductive success among colonies.

		Average success/colony (%)[a]				
Year	No. of colonies (No. of nests)	$\bar{x}$ ± SD	Range	χ^2	P	df[b]
1985	5 (164)	54.0 ± 15.9	29.5–71.4	13.5	<0.01	4
1986	15 (239)	75.9 ± 17.5	30.0–100.0	30.4	<0.01	14
1987	14 (248)	66.8 ± 14.4	50.0–90.9	18.2	>0.05	13
1988	15 (273)	58.8 ± 22.2	22.7–92.3	41.7	<0.001	14
1989	8 (148)	55.8 ± 16.2	33.3–74.1	12.7	>0.05	7
1990	5 (119)	65.7 ± 12.6	48.0–80.0	4.9	>0.05	4

[a] Success is percentage of nests fledging at least one bird.
[b] df is one less than the number of colonies.

TABLE 3. Sources of mortality to Boat-tailed Grackle eggs and young, 1985–1991.

Mortality source	Eggs (n = 1085)[a]		Young (n = 1117)	
	Mean[b] ± SD	Range	Mean ± SD	Range
Unhatched	18.7 ± 5.8	14.0–29.1	—	—
Abandoned	20.6 ± 9.6	9.5–38.5	7.7 ± 4.1	2.1–14.8
Depredated	42.1 ± 15.5	13.6–58.0	25.3 ± 7.4	14.3–34.5
Starved	—	—	52.1 ± 8.5	40.3–60.0
Nest collapsed	7.1 ± 4.0	0–10.5	8.3 ± 5.7	0–12.8
Other[c]	11.5 ± 7.2	0.7–23.5	6.5 ± 4.7	0–11.7

[a] Sample sizes refer to numbers of failed eggs and young.
[b] Means are percentages, averaged over seven years.
[c] Included losses from alligators basking in cattails, eggs removed by females, death from parasites, and eggs or young destroyed by human observers.

bing (13% of 67 mobbing incidents). Predators ranged in size from Fish Crows to Great Blue Herons (*Ardea herodias*).

To test for seasonal variation in nest success, I divided the breeding period into seven 2-week periods. Mean clutch size did not change signficantly over the season (F = 1.26; df = 7, 1392; $P > 0.05$). However, mean number of fledglings per nest varied significantly over the breeding season (F = 3.70; df = 7, 1392; P = 0.001). While clutch size remained the same, the average number of fledglings decreased as the season progressed (Fig. 1)

The proportion of nests lost to predators was low at the start of the nesting season, but the proportion increased as the season progressed (Fig. 2). In the first three weeks of the 1986–1989 nesting seasons (29 March–18 April), 1.6% of 959 nests were depredated. In the middle of the nesting season (17 May–6 June), 8.2% of the 943 remaining nests were depredated (Fig. 2). In three of the four years, the proportion of nests depredated varied significantly between months (1986: χ^2 = 1.0, $P < 0.05$, df = 3; 1987: χ^2 = 11.3, $P < 0.01$, df = 3; 1988: χ^2 = 26.0, $P < 0.001$, df = 3).

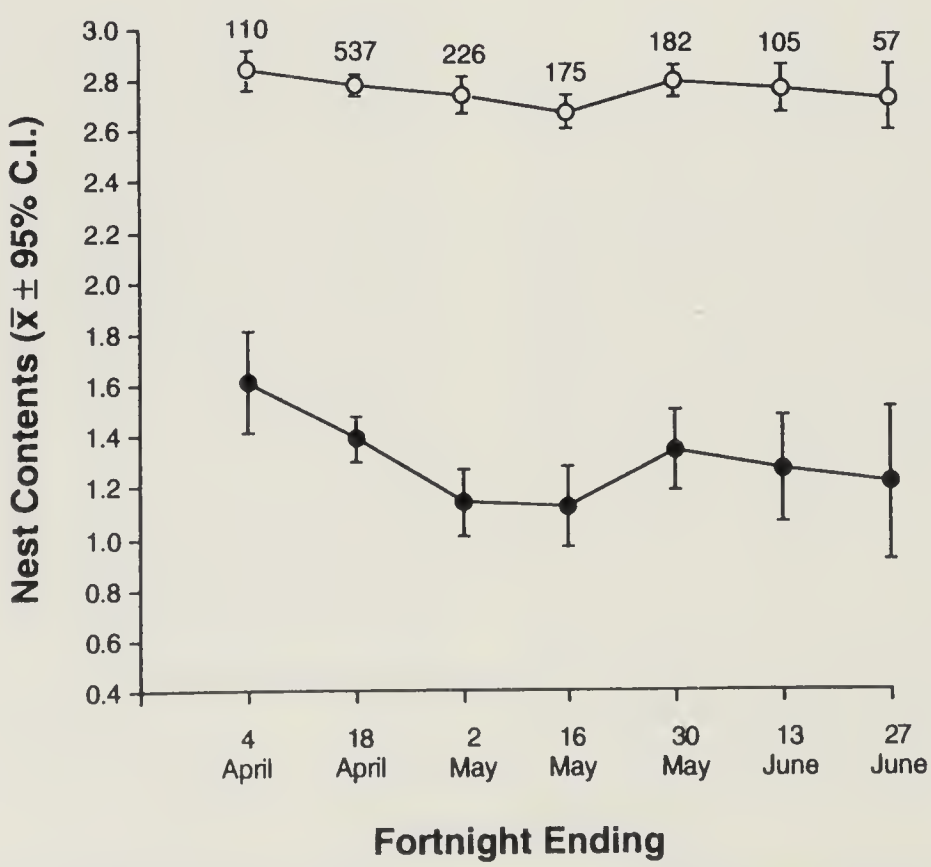

FIG. 1. Seasonal variation in clutch size (open circles) and number of fledglings (closed circles) per nest, 1985–1991. Sample size for each fortnight is given at top of figure. Sample size = 1392 nests.

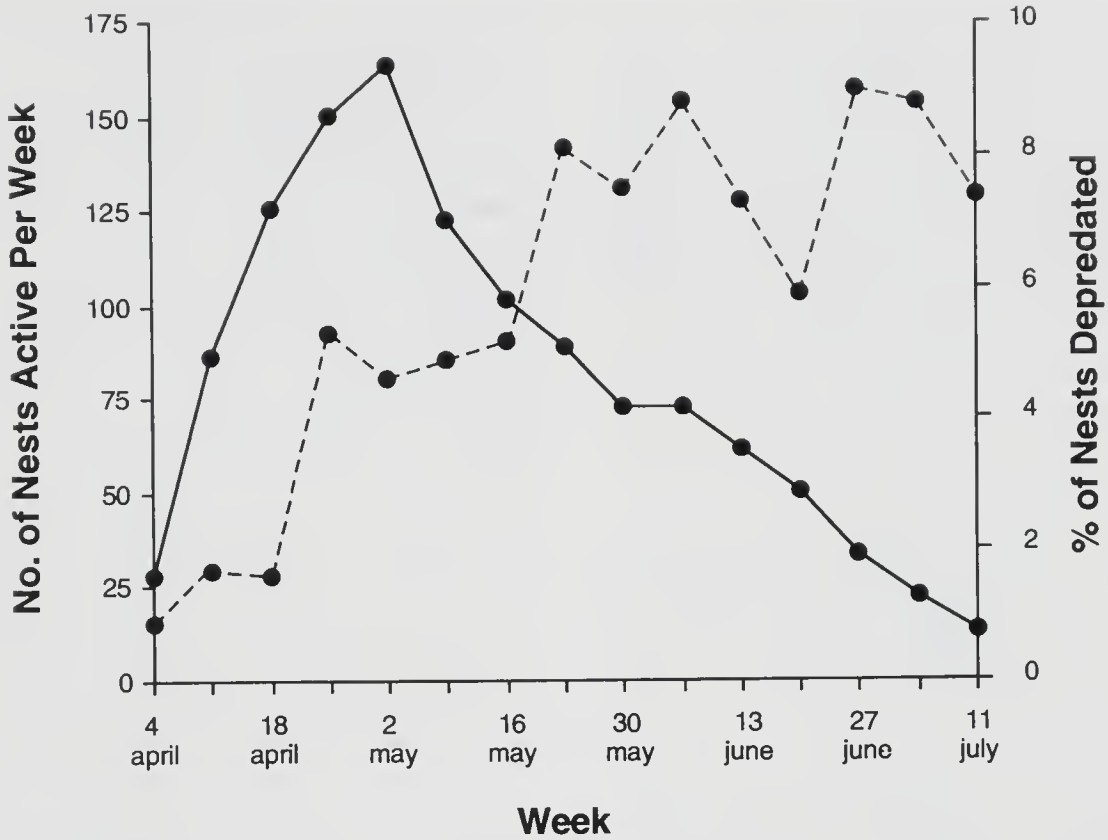

FIG. 2. Number of nests active per week (solid line), compared with proportion of nests depredated (dashed line), 1986–1989. Sample size (total no. of weeks that nests were exposed to losses) = 1902.

Foraging of colony-nesting females.—Females foraged away from the colonies, during low tide in adjacent river marshes, and during high tide in suburban and urban habitats 0.5–2.0 km away. Females did not follow each other to feeding areas, as indicated by associations between individuals leaving and entering the colonies. During 14.5 h of observation of five colonies, I recorded 718 foraging flights by individual females (401 leaving and 317 flights entering colonies). Only 20 flights out involved groups (19 pairs, one trio; 10% of all individual flights out). Similarly, I saw only 16 group flights into colonies (all involving pairs; 10% of all individual flights in).

As would be the case if females were foraging independently of each other, most of the food items brought to nests were arthropods that were widely dispersed in and around the study area. The most important (by frequency occurrence) dietary items collected from nestlings (n = 290 items from 43 nests, 25 Apr–1 Jun) were: adult Odonata, mainly Libellulidae, 16%; adult Diptera, mainly Stratiomyidae, 14%; Arachnida, mainly Lycosidae, 15%; Odonata naiads, 7%; adult Coleoptera, 8%; Orthoptera, mainly Acrididae, 7%; fish (*Menidia* and *Fundulus*), 4%; larval Diptera, mainly Stratiomyidae, 4%. Nestlings also received frogs (*Hyla cinerea* and *Rana utricularia*) and skink (*Eumeces* sp.) egg masses. Although not picked up in the samples, *Anolis* lizards were seen delivered to nests.

I found no correlation between number of young in a colony and percentage of young starving (1986: r = 0.32, n = 16 colonies; 1987: r = 0.35, n = 13; 1988: r = 0.11, n = 17; 1989: r = 0.29, n = 11; $P > 0.05$ for each year).

DISCUSSION

The hypothesis that colony nesting and solitary females have the same reproductive success (RS) is rejected. At least in some years, the RS of female Boat-tailed Grackles is enhanced by colony nesting. Over a 5-year period (1986–1990) colony nesting females had an average nest success (percentage of nests with at least one fledgling) of 63%, compared to 37% for contemporaneous solitary nesting females. Males only associated with solitary females during the 3-day period of sexual receptivity. After that, when an avian predator

approached their nests, these females often attacked alone. Males were always in attendance at colonies (Post 1992). At least in some years, male mobbing may be advantageous to colony females. Further, the protection that colony females gained from male mobbing appeared to have an all-or-nothing effect; RS was independent of colony size (Post 1994). An alternative explanation for the different RS of colony and solitary females is that the latter differ from the former in some trait such as food gathering ability. However, nestling starvation, which could be used as a measure of female quality, accounted for a larger proportion of nestling mortality in colonies than it did among solitary females: 27% of mortality in colonies was assigned to starvation vs 16% for solitary females ($\chi^2 = 5.84$, $P < 0.05$, df = 1).

It is possible that female Boat-tailed Grackles nest together because appropriate nest sites are limited (Bancroft 1987). In Florida cattail marshes, where rodent predation was the main cause of nest mortality, the vegetative structure (microhabitats) of depredated and successful grackle nest sites differed (Dunham 1990). But, in the cattail habitat I studied, appropriate macrohabitats (colony sites) were in surplus. Cattail islands having the same structural characteristics as contemporaneous colony sites were unoccupied. The idea that nesting habitat was not limited is further supported by findings that female grackles do not compete for nest sites (Post 1994).

As predicted, RS varied significantly between colonies. Over the six year period, the mean annual difference between the most successful and least successful colony was 49%. Variation in RS between colonies was mainly due to differences in predation rates. Reproductive success within colonies was not related to nest density, colony size, nor to intervals between nest starts (Post 1994). This lack of correlation may be due to the density independent effect of ground predators and the effectiveness of male grackles in deterring avian predators. Males are able to exclude diurnal avian predators from colonies, but they cannot protect nests from ground predators, which are active at night. When a colony was invaded by snakes, many females abandoned their nests and joined other colonies. The all-or-nothing effect of predation contributed to intercolony variation in RS.

In most colonies, large numbers of females were simultaneously receptive and overall synchrony within colonies was high (Post 1994). Numbers of nests peaked early in the season and, as numbers decreased, increasingly higher proportions of nests were depredated. This pattern suggests that predators found colonies gradually. By nesting early, grackles may be able to get a head start on predators (Wiley and Wiley 1980) or predators may initially be satiated (Hoogland and Sherman 1976). Alone or in combination, these factors would favor temporal clumping of nests. Other mortality factors, though independent of nest density, also favor early nesting. Nests built in April had fewer live support stems than those built in July (0.1 vs 1.9; Post 1995). Nests that are attached to living cattails stems are more likely to tilt because of different growth rates of stems (Bancroft 1987). Further, later nests were higher than early ones (88.7 cm vs 32.9 cm), which made them more likely to be blown down in storms (Post and Seals 1991). Herons roosted on some colony islands in late June and many grackle nests in these localities were destroyed by the herons (see also Bancroft 1987). Late nests were also subject to interference by grackle fledglings from earlier nests. Until they could fly, fledglings moved around island colony sites up to 30 days after leaving the nest (Bancroft 1987). Fledglings perched on nests, and trampled and defecated on eggs and small nestlings.

If female quality varied significantly among colonies, it would be expected that in at least some years, starvation, which is a measure of females' food-gathering ability, would vary between colonies. Starvation, however, varied little between colony sites. Food available for nestlings is probably not a determinant of breeding chronology. Initiation of breeding may be related primarily to females' ability to build up enough protein reserves for egg formation (Perrins 1970, Greenlaw 1978). It is unlikely that female grackles would be able to modify their reproductive behavior to reduce the effects of starvation.

Colonies do not appear to be formed as a means of improving foraging efficiency (Horn 1968, Bayer 1982). Female grackles fed nestlings prey that appeared to be evenly dis-

persed in and around the study area. It is unlikely that females foraging for such prey would benefit by following each other, as they would if they were feeding at concentrations of food (Horn 1968). Further, it is unlikely that females were exchanging information on the location of food, as only 10% of them left colonies together on feeding flights. In addition, the findings that starvation rates did not vary according to colony size and did not change over the season, indicate that food availability is not a critical factor in determining nest dispersion. Finally, females nesting together do not coordinate their breeding activities, such as might be the case if they benefitted from cooperative feeding (Post 1994).

Female Boat-tailed Grackles nest on marsh islands or isolated trees over land (Post et al. 1996), which are relatively safe from snakes and mammals. In addition to grackles, other species of large, sexually dimorphic blackbirds (oropendolas and caciques, *Psaracolius* and *Cacicus*) aggregate in isolated trees, apparently as a means of avoiding predators (Chapman 1929, Schäfer 1957, Drury 1962, Robinson 1985, Fraga 1989, Webster 1994). As in Boat-tailed Grackles, female caciques appear to have a surplus of appropriate nest sites, and site selection is more influenced by site tenacity than by physical differences between sites (Feekes 1981).

The behaviors related to coloniality in female Boat-tailed Grackles appear to occur as a response to predation. Colony sites are not limited, but females apparently follow each other to settle in appropriate (predator-safe) sites. Within colonies, females do not coordinate their breeding activities or foraging behavior. However, as a result of early breeding by females and, possibly, their common attraction to colony sites, overall synchrony of breeding is high. The temporal and spatial aggregation of female grackles allows individual males to sequester entire colonies.

Although males do not appear to influence where females settle to breed (Post 1994), the spacing and timing of breeding allow dominant males to monopolize entire colonies. The fitness of an individual male is determined mainly by the size of the female group that he sequesters, and the overall RS of that group. This may be critical for the evolution of harem polygyny in this species.

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VERTICAL DISTRIBUTIONS OF BREEDING-SEASON BIRDS: IS HUMAN INTRUSION INFLUENTIAL?

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ABSTRACT.—Human intrusion has become a widespread and chronic disturbance for birds in many wildlands. Because bird species often seek refuge, feed, and nest only in certain vegetation strata, intrusion-induced changes in vertical distributions could reduce access to such strata, increase interspecific competition, heighten energetic expenditures, and reduce nesting success. In Wyoming subalpine forests during the breeding seasons of 1989–1993, we studied the effects of intrusion on vertical distributions of Mountain Chickadees (*Parus gambeli*), Ruby-crowned Kinglets (*Regulus calendula*), Yellow-rumped Warblers (*Dendroica coronata*), and Dark-eyed Juncos (*Junco hyemalis*). Intrusion by one person for 1–2 h/week, similar in intensity to intrusion from some wildland recreationists and ecotourists, did not appreciably affect distributions of any of the species in three vegetation strata above the ground: less than 0.5 m, 0.5–3.0 m, more than 3.0 m. Although human disturbance has caused an increase in the height at which bird species in various habitats nest and roost, we found little evidence that intrusion altered vertical distributions of four passerines that nest, forage, sing, and seek refuge in subalpine forest. The minimal effects we observed indicate that the species we studied were able to tolerate low levels of intrusion. Studies of intrusion levels that do and do not affect vertical distributions are necessary to define the range of intrusion intensity that is influential. *Received 12 Jan. 1998, accepted 25 June 1998.*

Many bird species use specific vertical strata for nesting, feeding, and shelter (Dunlavy 1935, Colquhoun and Morley 1943, Preston and Norris 1947, MacArthur 1958, Cody 1985, Martin 1988). Vertical stratification is believed to partition resources and thereby reduce competition among coexisting species (Anderson et al. 1979). One factor that might alter vertical stratification is human intrusion. Intrusion is a pervasive and chronic disturbance that occurs even in protected habitats (Anderson and Keith 1980, Burger and Gochfeld 1991, Gutzwiller et al. 1994), and its effects on birds can include significantly lower reproduction and survival, displacement from crucial habitats, and abnormally high amounts of vigilance that reduce time for other essential activities (Boyle and Samson 1985, Burger and Gochfeld 1991, Knight and Gutzwiller 1995). For some bird species, human disturbance can also cause birds to increase nest height above the ground (Stoner 1937, Preston and Norris 1947, Anderson and Keith 1980, Knight and Fitzner 1985, Datta and Pal 1993).

One would expect a species' characteristic vertical location during breeding periods to reflect energetic efficiency of movements to nests, food sources, and shelter. Short flights between foraging substrates can cost more than 20× the energy used while resting (Goldstein 1990), so repeated flights to vertical strata that are atypical for a species could be maladaptive (Dhindsa et al. 1989). Disruption of vertical distributions may thus have significant impacts on competitive relations among species, energy budgets, and hence fitness.

As an initial assessment of whether intrusion could cause such changes, we tested for intrusion effects on vertical distributions. Because low levels of intrusion in wildlands are more ubiquitous than are intense levels of intrusion, low levels have the potential to affect more individuals and species (Gutzwiller et al. 1994). Therefore, we examined whether low levels of intrusion (1–2 h/week) caused sustained effects on vertical distributions of birds in three vegetation strata above the ground: less than 0.5 m (stratum 1), 0.5–3.0 m (stratum 2), more than 3.0 m (stratum 3). Our ob-

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jective was to determine whether intrusion would displace birds from strata 1 and 2, where disturbance from a walking intruder is most intense, into stratum 3.

METHODS

Study area.—Data were collected approximately 70 km WNW of Laramie, Wyoming (41° 32′ N, 106° 20′ W) in the Snowy Mountains. Plant communities, elevations, and weather conditions are described in Gutzwiller and coworkers (1997). In May 1989, we randomly established 30 circular 1.0-ha (113-m diameter) sites for the 5-year study. Sites were 0.4 km from the nearest used road and were an average of 0.7 km apart.

Intrusion treatments.—We randomly assigned intrusion treatments to the 1.0-ha sites during May 1989; the same assignments were used during all 5 years. Treatments involved two levels of frequency [one (F1) or two (F2) intrusion treatments/week], two levels of spatial scale [the inner 25% (S25) or 100% (S100) of the site was intruded], and controls (no intrusion treatments). The five groups were replicated as follows: F1-S25 (n = 5); F1-S100 (n = 5); F2-S25 (n = 5); F2-S100 (n = 5); Control (n = 10). In the present analysis, we were only interested in whether the intrusions in general were influential, so we grouped all disturbed sites into a single group called intruded sites. F1 treatments were implemented on Wednesdays and F2 treatments were administered on Mondays and Fridays so treatments would not coincide with bird sampling, which occurred on Tuesdays and Thursdays.

Each year for 10 weeks between late May and early August, each treated site was intruded an equal number of times during various times of day between 07:00–15:00 MST. A single intrusion treatment involved one person walking through the site in a radial pattern, beginning when the person reached the marked perimeter of the 1.0-ha site. Movements were made from the site center (marked) to the perimeter and back again; directions of movement were shifted approximately 40° after each return to the center, and the specified area was covered twice during a 1-h period. Additional details about intrusion treatments are in Gutzwiller and coworkers (1997).

Bird sampling.—Data for the present analysis were gathered with the sampling techniques described by Riffell and coworkers (1996) and Gutzwiller and coworkers (1997). When investigators reached the marked 1.0-ha perimeter, they began recording the vertical position (stratum 1, 2, or 3) of birds inside the 1.0-ha site. They continued to record these data as they proceeded toward the site center where they completed the 15-min count. When a bird was heard but not seen, investigators could not always clearly ascertain its vertical location; the present analysis involves only birds for which the vertical stratum was known. Half of the sites were sampled on Tuesdays and half on Thursdays each week. Daily timing, weather conditions, and randomization for sampling are described elsewhere (Gutzwiller et al. 1997).

Habitat features.—If differences in habitat features were confounded with treatment groups, effects of intrusion on vertical distributions would not be distinguishable from those caused by habitat conditions. We measured a variety of habitat variables and found that none differed between control and intruded sites during any year (details in Gutzwiller et al. 1997), indicating that habitat features were not confounded with treatment groups.

Statistical analyses.—For each year, site, and stratum separately, we computed the total number of individuals detected for four species that occurred on at least 19 of the 30 sites: Mountain Chickadee (*Parus gambeli*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Dendroica coronata*), Dark-eyed Junco (*Junco hyemalis*). These four species were sufficiently abundant to allow us to detect differences in vertical distributions. To avoid the problem of pseudoreplication that would have been incurred if we had treated individual observations of birds as independent, our experimental unit was a site. Because intrusion may have displaced birds from an entire site, those sites that did not have detections for a species within any of the three strata for a given year were not used in analyses for that species and year. This approach reduced the possibility that changes in vertical distributions would be confounded in our analyses with displacement effects.

The normality assumption of Student's t-test and Welch's t-test was not always tenable. Consequently, for each species, year, and stratum separately, we used Mann-Whitney U statistics (Zar 1996) from BMDP 3D software (1990 release, VAX mainframe, Dixon 1990) to test the following *a priori* 1-tailed research hypotheses: for strata 1 and 2, number of birds detected on control sites is greater than that on intruded sites; for stratum 3, number of birds detected on control sites is less than that for intruded sites. As recommended by Zar (1996), U' was used to test the hypotheses for strata 1 and 2, and U was used to test the hypothesis for stratum 3. We reported group means because in most cases the mean was the best descriptor of central tendency. We did not use repeated measures ANOVA for the reasons given by Gutzwiller and coworkers (1997). We did not combine all of the data into one set and conduct a single standard ANOVA because possible site fidelity by individual birds and small changes in the physical sites made it inappropriate to assume that our experimental units were sufficiently independent among years. Using separate Mann-Whitney tests, we did not have to make any untenable or questionable assumptions and there was no pseudoreplication within or among years.

We used an *a priori* $\alpha = 0.10$ instead of 0.05 for all analyses to improve statistical power (Westmoreland and Best 1985). To control for Type I error, we used a sequential Bonferroni adjustment of α for simultaneous inferences (Holm 1979, Rice 1989). For each species and year, we tested a set of three simultaneous hypotheses, one for each of the three strata. We considered each set to be a "family" (Miller 1981)

TABLE 1. Mean number of individuals for four species on control sites at three vertical strata, 1989–1993. Each value is a 5-year mean of the number of individuals per vertical meter of stratal height span (0.5 m for stratum 1; 2.5 m for stratum 2; 12 m for stratum 3).

Species	Vertical stratum (m)		
	<0.5	0.5–3.0	>3.0
Mountain Chickadee	0.4	4.5	1.8
Ruby-crowned Kinglet	0.4	1.8	2.4
Yellow-rumped Warbler	0.0	1.6	1.9
Dark-eyed Junco	17.6	8.6	1.5

of hypotheses. The sequential α levels for significance within a family were 0.033, 0.05 and 0.10.

We determined whether our sampling method provided data on vertical habitat use that were consistent with the strata the species are known to use during the breeding season in the absence of repeated intrusion. Control-site data for the four species were used for this analysis. For each species, year, and stratum separately, we tallied the total number of individuals. Because the three strata had different vertical extents, the number of individuals recorded for the three strata were not directly comparable. To determine relative concentrations of individuals among the strata, we computed the total number of individuals for a given species, year, and stratum on a per meter basis, dividing stratum 1 totals by 0.5 m (0.5 − 0.0 m = 0.5 m), stratum 2 totals by 2.5 m (3.0 − 0.5 m = 2.5 m), and stratum 3 totals by 12 m. The latter span of height reflected the possibility that the highest nests were 15 m above the ground (15 − 3 m = 12 m), the approximate height of nest substrates in the canopy at our sites. For each species and stratum, we calculated a 5-year mean for the number of individuals/m; we compared the resulting vertical distributions with those expected based on published heights for foraging and nesting.

A general estimator to calculate minimum detectable effect sizes for Mann-Whitney tests is not available. Consequently, we programmed simulations with FORTRAN to determine effect sizes, which were the smallest between-group differences in the number of individuals that we could have detected as statistically significant. For each species, year, and stratum, we used an iterative trial-and-error method to find the smallest difference in number of individuals that led to a significant U value 80% of the time at $\alpha = 0.033$ and at $\alpha = 0.10$ (the minimum and maximum α levels possible for each family of hypotheses). We simulated scores from distributions that mimicked observed sample distributions. Once the underlying distributions were established, scores were randomly drawn from them and the Mann-Whitney U was calculated. We repeated this step 10,000 times and computed the percentage of these iterations in which the null hypothesis was rejected.

RESULTS

Assessment of vertical sampling.—During the 5-year period, species were detected on control sites to varying extents in the three strata (Table 1).

Vertical distributions.—Most tests indicated no differences in number of individuals between control and intruded sites (Tables 2–5). The only statistically significant effect oc-

TABLE 2. Summary statistics and results of Mann-Whitney tests for number of Mountain Chickadees on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n)		U', U[a]	P
		Control	Intruded		
1989	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (15)	—[b]	—[b]
	0.5–3.0	2.90 ± 0.91 (10)	1.53 ± 0.38 (15)	91.5	0.191
	>3.0	1.30 ± 0.21 (10)	2.07 ± 0.52 (15)	89.0	0.231
1990	<0.5	0.00 ± 0.00 (6)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.33 ± 0.33 (6)	0.06 ± 0.06 (18)	60.5	0.349
	>3.0	2.83 ± 0.91 (6)	3.61 ± 0.53 (18)	68.0	0.189
1991	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (16)	—	—
	0.5–3.0	0.38 ± 0.26 (8)	0.25 ± 0.11 (16)	66.0	0.464
	>3.0	2.75 ± 0.75 (8)	2.56 ± 0.29 (16)	63.5	0.524
1992	<0.5	0.10 ± 0.10 (10)	0.00 ± 0.00 (17)	93.5	0.347
	0.5–3.0	1.20 ± 0.59 (10)	0.88 ± 0.23 (17)	83.5	0.539
	>3.0	4.00 ± 1.18 (10)	2.94 ± 0.42 (17)	82.0	0.568
1993	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (20)	—	—
	0.5–3.0	1.00 ± 0.26 (10)	1.15 ± 0.21 (20)	93.5	0.619
	>3.0	1.70 ± 0.26 (10)	2.40 ± 0.45 (20)	111.5	0.317

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.
[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

TABLE 3. Summary statistics and results of Mann-Whitney tests for number of Ruby-crowned Kinglets on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n) Control	Intruded	U', U[a]	P
1989	<0.5	0.11 ± 0.11 (9)	0.05 ± 0.05 (19)	90.5	0.414
	0.5–3.0	0.89 ± 0.48 (9)	0.42 ± 0.16 (19)	94.0	0.350
	>3.0	5.67 ± 1.22 (9)	3.63 ± 0.58 (19)	60.0	0.897
1990	<0.5	0.00 ± 0.00 (6)	0.00 ± 0.00 (15)	—[b]	—[b]
	0.5–3.0	0.17 ± 0.17 (6)	0.40 ± 0.13 (15)	34.5	0.799
	>3.0	3.17 ± 0.60 (6)	2.00 ± 0.35 (15)	23.0	0.960
1991	<0.5	0.00 ± 0.00 (9)	0.00 ± 0.00 (15)	—	—
	0.5–3.0	0.22 ± 0.15 (9)	0.47 ± 0.19 (15)	58.0	0.721
	>3.0	3.33 ± 0.62 (9)	4.13 ± 0.57 (15)	84.0	0.174
1992	<0.5	0.00 ± 0.00 (9)	0.00 ± 0.00 (17)	—	—
	0.5–3.0	0.78 ± 0.36 (9)	0.65 ± 0.31 (17)	85.0	0.336
	>3.0	2.33 ± 0.75 (9)	2.65 ± 0.45 (17)	91.5	0.221
1993	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.50 ± 0.27 (8)	0.56 ± 0.18 (18)	70.0	0.554
	>3.0	2.75 ± 0.73 (8)	2.39 ± 0.47 (18)	62.5	0.707

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.
[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

curred during 1990 for Dark-eyed Juncos, which were more abundant in stratum 1 on control sites than they were in this stratum on intruded sites (Table 5).

Effect sizes.—Minimum detectable effect sizes were an average of 1.05–2.11 times ($\alpha = 0.033$) and 0.84–1.71 times ($\alpha = 0.10$) the magnitude of control-site means of the original data (Table 6). Differences in number of individuals of these magnitudes and larger would have been detectable with a probability of 0.80; smaller differences were detectable with less reliability.

DISCUSSION

Assessment of vertical sampling.—The midpoint of the usual nest-height range for Mountain Chickadees is 3.2 m above the ground (Terres 1980) and, for much of their food, Mountain Chickadees glean insects from fo-

TABLE 4. Summary statistics and results of Mann-Whitney tests for number of Yellow-rumped Warblers on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n) Control	Intruded	U', U[a]	P
1989	<0.5	0.00 ± 0.00 (7)	0.14 ± 0.10 (14)	42.0	0.708
	0.5–3.0	0.29 ± 0.18 (7)	0.21 ± 0.11 (14)	52.5	0.414
	>3.0	2.00 ± 0.49 (7)	1.64 ± 0.29 (14)	40.0	0.756
1990	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (13)	—[b]	—[b]
	0.5–3.0	0.13 ± 0.13 (8)	0.46 ± 0.22 (13)	41.5	0.783
	>3.0	1.88 ± 0.44 (8)	1.85 ± 0.25 (13)	54.0	0.458
1991	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (15)	—	—
	0.5–3.0	0.30 ± 0.15 (10)	0.60 ± 0.25 (15)	68.0	0.656
	>3.0	2.90 ± 0.60 (10)	3.20 ± 0.49 (15)	82.5	0.352
1992	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (19)	—	—
	0.5–3.0	0.60 ± 0.34 (10)	0.89 ± 0.27 (19)	80.0	0.758
	>3.0	3.70 ± 0.96 (10)	3.53 ± 0.61 (19)	95.5	0.500
1993	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.80 ± 0.29 (10)	1.28 ± 0.31 (18)	73.5	0.789
	>3.0	1.90 ± 0.28 (10)	2.17 ± 0.34 (18)	95.5	0.407

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.
[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

TABLE 5. Summary statistics and results of Mann-Whitney tests for number of Dark-eyed Juncos on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n) Control	Mean ± SE (n) Intruded	U', U[a]	P
1989	<0.5	1.00 ± 0.55 (9)	2.06 ± 0.49 (17)	47.5	0.943
	0.5–3.0	4.00 ± 1.07 (9)	1.76 ± 0.43 (17)	110.0	0.037
	>3.0	0.67 ± 0.29 (9)	0.65 ± 0.23 (17)	74.0	0.563
1990	<0.5	0.67 ± 0.21 (6)	0.08 ± 0.08 (13)	62.0	0.023[b]
	0.5–3.0	0.67 ± 0.21 (6)	1.00 ± 0.28 (13)	33.0	0.711
	>3.0	1.67 ± 0.67 (6)	1.23 ± 0.30 (13)	33.5	0.696
1991	<0.5	0.70 ± 0.34 (10)	0.94 ± 0.35 (18)	85.0	0.602
	0.5–3.0	1.60 ± 0.60 (10)	1.83 ± 0.51 (18)	84.0	0.620
	>3.0	3.00 ± 0.37 (10)	2.89 ± 0.44 (18)	76.5	0.746
1992	<0.5	1.00 ± 0.60 (10)	0.95 ± 0.35 (20)	98.5	0.534
	0.5–3.0	2.90 ± 0.62 (10)	4.30 ± 0.82 (20)	80.0	0.813
	>3.0	3.50 ± 0.79 (10)	2.30 ± 0.36 (20)	70.0	0.909
1993	<0.5	1.40 ± 0.76 (10)	1.60 ± 0.29 (20)	70.0	0.909
	0.5–3.0	2.20 ± 0.59 (10)	1.70 ± 0.33 (20)	115.0	0.265
	>3.0	0.70 ± 0.34 (10)	1.10 ± 0.20 (20)	127.5	0.120

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.
[b] P value was significant at a family-wide $\alpha = 0.10$ after a sequential Bonferroni adjustment.

liage (DeGraaf et al. 1991). Most foliage at the study sites was associated with saplings and trees of aspen (*Populus* spp.) and conifers and occurred in strata 2 and 3. Nests are typically near the boundary of strata 2 and 3, so movements near the nest within strata 2 and 3 would be common. Most Mountain Chickadees were detected in strata 2 and 3, which is consistent with their breeding-season habitat use.

The midpoint of the typical nest height range for Ruby-crowned Kinglets is 15.6 m (Terres 1980). One common component of their nests is rootlets, which are obtained at ground level. This species typically gleans or hawks insects and spiders (DeGraaf et al. 1991) at the tips of branches, around twigs, and occasionally in vegetation near the ground (Terres 1980). Because its nest is high and it tends to search upper layers of foliage for food, one would expect to detect most Ruby-crowned Kinglets in stratum 3, fewer in stratum 2, and the fewest in stratum 1. This is the pattern we observed.

Yellow-rumped Warblers have a range midpoint of 8.1 m for nest height (Terres 1980). They usually glean and flycatch from vegetation layers that are high above the ground (Curson et al. 1994), but individuals may fly vertically from bushes to flycatch (Terres 1980). Yellow-rumped Warblers often vocalize from the tops of pines and firs (Terres 1980). Given this information, one would expect few if any individuals to occur in stratum 1, more to occur in stratum 2, and most to occur in stratum 3. Our results are consistent with these expectations.

Typically, Dark-eyed Juncos nest on or near the ground and forage for seeds and insects at or near ground level (Terres 1980, Farrand 1983, DeGraaf et al. 1991). Consistent with these generalizations, we detected most Dark-eyed Juncos within stratum 1, fewer in stratum 2, and fewest in stratum 3.

Our observations on control sites were in close accord with the breeding season habitat use and foraging behaviors of these four species. These results indicate that the method we used to record vertical locations accurately reflected distributions and therefore provided ecologically relevant data. Evidently, practicing before collecting data and using only those observations about which an investigator was confident effectively controlled errors in height estimation. The consistency between our observations on control sites and species' typical vertical distributions also supports previous evidence (Gutzwiller et al. 1994, Riffell et al. 1996) that the sampling technique itself was not intrusive.

Effect sizes.—Minimum detectable effect sizes indicated that we can be confident with

TABLE 6. Summary statistics for minimum detectable effect sizes for Mann-Whitney tests. Table entries are for all years and strata combined and are in terms of multiples of the magnitude of control-site means for the original data; individual effect sizes were divided by their associated control-site means before summary statistics were computed.

Species	Mean (range)	
	$\alpha = 0.033$	$\alpha = 0.100$
Mountain Chickadee	2.11 (0.91–5.40)	1.71 (0.83–4.30)
Ruby-crowned Kinglet	1.86 (0.57–4.91)	1.48 (0.49–4.00)
Yellow-rumped Warbler	1.18 (0.61–2.21)	0.97 (0.55–1.76)
Dark-eyed Junco	1.05 (0.77–1.34)	0.84 (0.61–1.00)

a probability of 0.80 that few large changes in the vertical distributions of birds were caused by the intrusions we administered. Only large differences were likely to be detected, however, so the single significant effect reported here should be regarded as a conservative estimate of the effects of intrusion on vertical distributions.

Vertical distributions.—Several biological reasons are plausible for the lack of change in vertical distributions. First, bird sampling at all sites occurred an average of 2.0–3.5 days after treatments, and it is possible that changes induced during treatments did not last long enough to be detected during subsequent sampling. Second, individuals that were displaced from their characteristic strata may have been replaced by other territory seeking conspecifics not yet exposed to the intrusion treatments. Third, individuals chased from their typical vegetation layers may have had their undefended nests preyed upon (see Boyle and Samson 1985); one consequence might have been site abandonment by these individuals and subsequent occupation by conspecifics that up to that time had been off site without territories. Fourth, unfavorable physical conditions (Adams 1941, Dhindsa et al. 1989), the number of existing territories, and interspecific competition may have prevented lower-strata species from using stratum 3. Nest type and migratory status did not seem to influence these species' sensitivities to intrusion (Riffell et al. 1996).

Human disturbance can cause birds to nest or roost higher above the ground than normal (Preston and Norris 1947, Anderson and Keith 1980, Knight and Fitzner 1985, Datta and Pal 1993). Higher nests can be more susceptible to wind damage (Knight and Fitzner 1985), may expose eggs and nestlings to winds and low temperatures, and may force adults to expend more energy to feed nestlings (Dhindsa et al. 1989). Because of less favorable physical conditions (Adams 1941), higher strata may not be energetically advantageous for foraging or refuges. For these reasons, it would be valuable to know the level of intrusion that would cause changes in vertical distributions. The levels of intrusion we experimented with were evidently too low to induce substantial or sustained effects, but higher levels of intrusion might be influential. A series of experiments involving a range of intrusion intensities would help identify threshold levels of intrusion. The absence of effects found in the present study helps define the level of intrusion that is not influential, at least for the species and conditions we studied.

We tested for intrusion effects on vertical distributions associated with all typical breeding season behaviors combined. Although this general approach was valuable, detections from some behaviors (e.g., singing) may have masked intrusion effects on strata used during other behaviors (e.g., foraging). For a more thorough assessment, experiments involving all behaviors combined and specific behaviors separately are needed. Serial experiments (Gutzwiller 1993) with various avian taxa, vegetation types, and intrusion intensities should be used to clarify whether vertical distributions are usually affected and, in turn, whether such changes reduce avian fecundity or survival.

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Symposium

ORNITHOLOGY IN NORTHERN CENTRAL AMERICA

EDWARD H. BURTT, JR.[1]

Northern Central America stretches from the northernmost Neotropical rainforest in the lowlands of the Isthmus of Tehuantepec south to the arid Pacific coast of Nicaragua and the pine savannahs of Honduras. Its biogeography is complex; the product of a tumultuous geological history in which climate change, the rise and fall of oceans, and the interaction of tectonic plates have all influenced the diversity of habitats and the evolution of Central American birds. Roughly one-third of the approximately 1070 species of birds that breed in northern Central America are endemic (Howell, S. N. G. and S. Webb. 1995. The birds of Mexico and northern Central America. Oxford Univ. Press, Oxford, U.K.). An additional 225 species of North American birds pass through or winter in the region. In recognition of those who have explored the ornithological complexity of northern Central America and in the hope of stimulating new research on the birds of this region, the Wilson Ornithological Society sponsored a symposium "Ornithology of northern Central America" at its 1995 annual meeting.

Fifty million years ago North and South America were separated by three large islands and four substantial water gaps. For the next 47 million-years, two distinct, tropical avifaunas flourished, each with ample opportunity for repeated cycles of geographic isolation and speciation across the islands and water gaps separating the continents. The rise of the Panamanian isthmus 3 million years ago coincided with climatic cooling. Northern tropical habitats retreated into the Central American lowlands and temperate habitats invaded the Central American highlands. The landscape was fragmented into isolated pockets of tropical lowlands, temperate highlands, and subtropical slopes. The land bridge also provided for extensive interchange of tropical species from North and South America. Multiplication and fragmentation of habitats led to explosive radiation of several avian families from tropical North America and from tropical South America.

Exploration of these ornithological riches dates from the independence of the Central American countries from Spain in the 1820s. Collectors sponsored by wealthy Europeans were the first explorers. The first comprehensive work on the region was begun in 1857 by Osbert Salvin and culminated in the publication of the 63-volume *Biologia Centrali Americana.* In Mexico the extensive field work of Nelson and Goldman from 1892 to 1906 laid the foundation for later studies of distribution and natural history, Also during this period Ridgway published the first comprehensive taxonomic and distributional guide to birds of the region. From 1950 into the 1990s ornithologists focused on systematics and distribution as critical to understanding the evolution of the Central American avifauna. Recently conservation of biodiversity has emerged as an important concern within the region, but the need for communication among those working in northern Central America is crucial to the success of conservation efforts. To stimulate communication the Wilson Ornithological Society organized and hosted the symposium "Ornithology in northern Central America" at its 1995 annual meeting. The speakers, who are the authors of the following papers, are among the foremost ornithologists working or living in the region.

While discussion at the occasional North American symposium is helpful, all speakers expressed the need to open lines of communication among Central Americans. Their agreement led to the idea of a Mesoamerican organization to promote the study of the natural history of northern Central America. In July 1995 Oliver Komar promoted the idea to about 50 conservation and biology professionals from El Salvador, Honduras, and Nicaragua. The organizational meeting was attended by 11 representatives of El Salvador and Honduras. The attendees drafted a proposal for the society, prepared and accepted an offer by Gerardo Borjas to host a founding meeting in Honduras in January 1996. Seventeen biologists from five countries attended the meeting at which the society's constitution was written, provisional officers were elected, and a quarterly bulletin established. About 70 persons attended a second meeting in June 1996 when bylaws and a mission statement were adopted. About 250 people attended the First Mesoamerican Congress for Biology and Conservation in Tegucigalpa, Honduras, and almost 400 attended the Second Congress in Managua, Nicaragua in June 1998. The bulletin, *Mesoamericana*, now appears quarterly. The Board of Directors of the Mesoamerican Society for Biology and Conservation includes representatives from all Central American countries and membership in the Society exceeds 400. The Wilson Ornithological Society can be proud of its role in facilitating the organization of the Mesoamerican Society through its symposium "Ornithology in northern Central America."

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HABITAT USE AND REPRODUCTIVE ECOLOGY OF THE OCELLATED TURKEY IN TIKAL NATIONAL PARK, GUATEMALA

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ABSTRACT.—Despite its size, color, importance as a game species, and restricted geographic range (Yucatán Peninsula, northern Belize, and northern Guatemala), little is known about the ecology of the Ocellated Turkey (*Meleagris ocellata*). Habitat use, breeding behavior, and survival based on radiotelemetry of this species were studied in Tikal National Park, Guatemala 1988–1989 and 1993–1994. Ocellated Turkeys use tall forest cover to care for their poults and forest clearings and other vegetation types during courtship and nesting. Radio-collared females traveled up to 8 km (average of 2.4 km) from the point of capture in search of nesting sites. Nesting success of eight hens was 62% and poult survival rate was 15%. The largest home range recorded for a female with poults was 12.5 km^2.

The Ocellated Turkey (*Meleagris ocellata*), one of the most spectacular birds in the Guatemalan avifauna, is an important game species that is commonly sought by subsistence hunters. The species occupies a relict geographic range that includes the Yucatán Peninsula, southern Tabasco and northeastern Chiapas in Mexico, northern Belize, and the lowlands of northern El Petén in Guatemala (Ogilvie-Grant 1893, Griscom 1932, Ridgway and Friedman 1946, Friedman et al. 1950, Leopold 1965, Lint 1977–1978, Steadman et al. 1979). This restricted range makes the species highly vulnerable to range reduction and habitat fragmentation. Since 1977, several authors have reported that populations have decreased and the species is now considered scarce in some areas, probably as a result of habitat loss, overharvest, and disease spread by domestic fowl (Lint 1977–1978, Steadman et al. 1979, Jennings 1987).

Most accounts of this species are general descriptions of occurrence and behavior. The only systematic field study on Ocellated Turkeys was performed by Steadman and coworkers (1979) during a three-week period in Tikal National Park. Biologists' lack of concern may be explained in part by the fact that the species was traditionally considered to benefit from secondary growth and forest clearings (Leopold 1965).

Information on habitat requirements of the Ocellated Turkey suggests that it uses savannas, marshlands, arid brush zones, ecotones between primary and secondary vegetation, milpas (small corn patches), forests with clearings, and other habitats. These vague descriptions suggest that the species requires a mix of forest and clearings to survive. However, it is unclear what forest and clearing types the turkeys use, in what proportion, during what times of the year, and for what activities. Without such information, it is not possible to predict the impact of extensive forest clearing on the species' population dynamics.

We studied habitat use and reproductive ecology of the Ocellated Turkey in response to the need for systematic, scientific information on a species that appears to be declining. The study consisted of two phases. The first phase was focused on habitat use and breeding behavior. The second phase was focused on habitat use by females and on population dynamics of females and poults.

STUDY AREA AND METHODS

Study area.—We studied turkeys in Tikal National Park (17° 33′ N, 89° 35′ W) in the northern part of the state of El Petén, Guatemala (Fig. 1). The Maya city of Tikal was one of the most prominent developments of the Mayan lowlands during the Classic Period (800 A.D.). Because of its archaelogical and ecological importance, Tikal was decreed a national park in 1955, with an area of 576 km^2 (Acuerdo Presidencial 1955). In 1990 Tikal National Park was absorbed as one of the fully protected nuclear zones in the Maya Bio-

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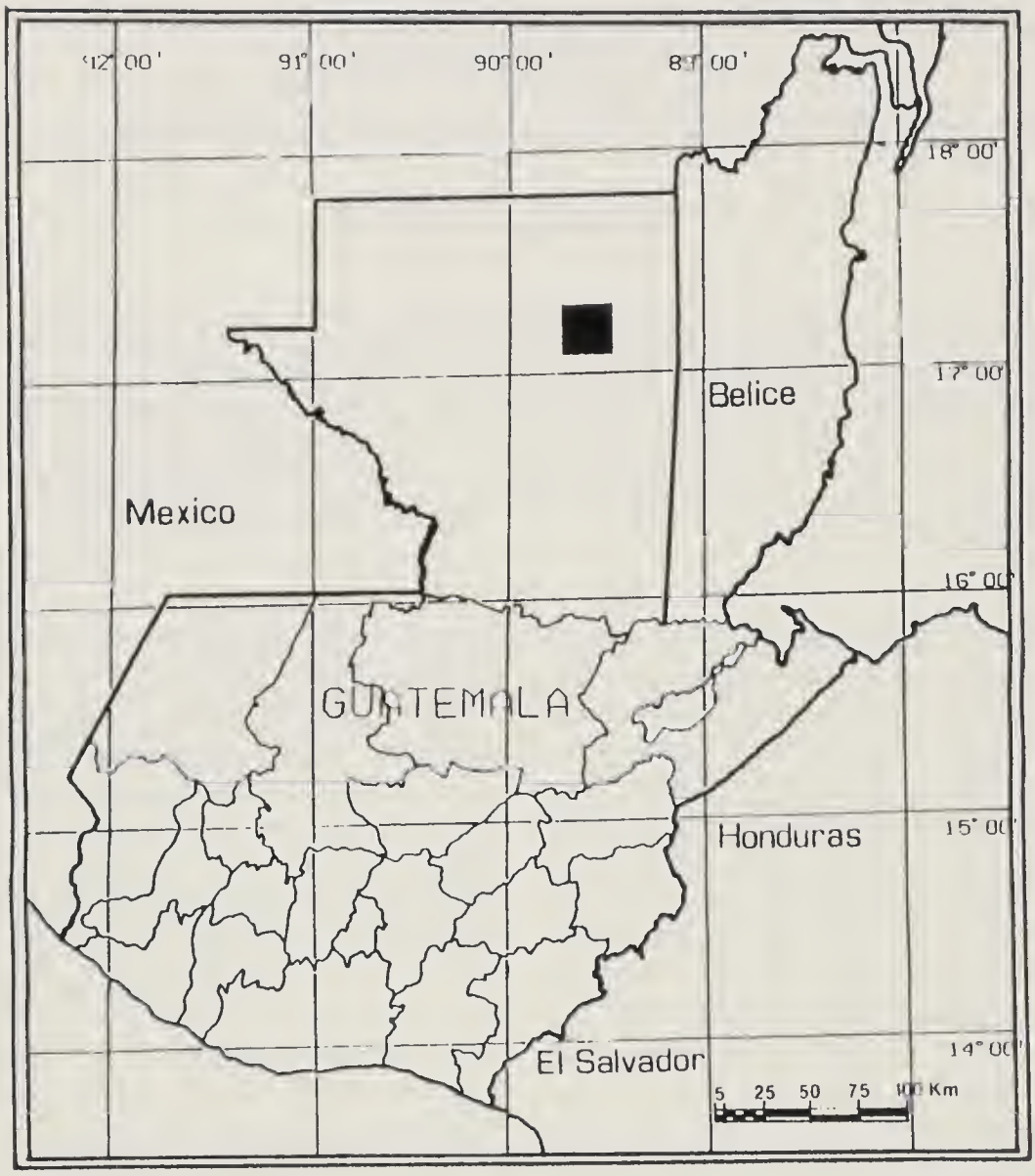

FIG. 1. Location of Tikal National Park, Guatemala.

sphere Reserve (Congreso de la República de Guatemala 1990), which protects 1.5 million ha in northern El Petén.

According to the Holdridge life-zone system, Tikal is located in warm subtropical humid forest (Instituto Geográfico Militar 1983). Temperature extremes range from 10° to 38° C. The hottest months are May and June, with daily maximums between 30° and 35° C, and minimums between 21° and 24° C. December through February are the coldest months with daily maximums between 24° and 27° C and minimums of 16° to 18° C. Temperatures as low as 2° C have been recorded. Annual precipitation is 1500–2000 mm. The rainy season usually begins in mid-May and ends in November. September and June are the rainiest months, and February and March are the driest with only 30–50 mm of rain. Heavy dawn mists during the dry season allow for green vegetation year round (National Park Service 1973).

Park topography is characterized by low undulating hills with a mean elevation of 300 m and the highest point 438 m. Soils are thin and the substrate is karstic, causing rapid runoff of surface water. Tikal has several natural depressions, locally called "bajos", or low forest, that may hold standing water during the rainy season and sometimes throughout the year. Areas that do not flood during the rainy season are known as "tall forest", and account for approximately 78% of the park area (National Park Service 1973).

Methods.—This study was divided into two phases, each with different objectives. General observations on behavior and appearance of the birds, particularly during the breeding season, were recorded throughout the project.

To provide the basic framework for habitat analyses, local expertise was utilized to define gross characteristics of the vegetation types. Five vegetation associations were identified and separated, mainly by species composition and soil hydrology.

In the first phase of the study, fifteen transects 1.2–2.0 km long were established among the different vegetation types for a total of 24.1 km. From December 1988 to July 1989 a team of four people, including MJG, walked the transects (at a speed of 1 km/hr) at

least once per month during morning hours (beginning within 1 hr of sunrise). We recorded sightings, vocalizations, and signs such as feathers and droppings, along with information on time of day, date, sex, and age (adult and yearling, if possible). We also observed and counted turkey flocks in the administrative and tourist area of Tikal monthly to obtain information on group size, age and sex composition, as well as behavior. Age and sex determination followed Smithe (1966) and Steadman and coworkers (1979). Changes in monthly composition of groups were examined with Kolmogorov-Smirnov tests ($P = 0.05$).

The second phase of the project (January 1993, to October 1994) was a study of habitat use by females and population dynamics of the species in Tikal. During January and February 1993–1995, we surveyed the administrative and ruins areas of Tikal for the occurrence of turkeys. We chose the Mundo Perdido (Lost World) ruins and the camping area as capture sites. Ocellated Turkeys were captured in Q-nets (Furman Diversified, Texas) and a custom-made drop net with a 5-cm mesh; both were baited with corn. Our trapping efforts were primarily directed toward females and restricted to a maximum of 2 hrs after daylight because high humidity combined with temperatures in excess of 25° C can cause stress and increased risk of mortality in turkeys. Measurements of weight, tail length, tarsus, and wing were taken of all captured birds prior to fitting them with harnessed backpack transmitters with a mortality/motion sensor. The radios (Mod-200 and Mod-300, Telonics, Inc., Arizona) weighed 103–130 gm and operated in the 150–151 MHz range. Expected life of the batteries was 24 months.

Following initial release, we located the radio-tagged turkeys daily with a hand-held yagi antenna and receiver ("H" antenna; Telonics, Mesa, AZ). Whenever possible, we took readings from elevated points, such as the Maya temple ruins. After poults hatched, a different female was located several times each day during peak activity hours; we also attempted direct observation. During periods of low activity each day, we located all the hens to determine their general area of activity. Radio-tracking continued through the brood rearing period or until the birds formed flocks, normally by September.

Locations were plotted on 1:25,000-scale maps. Preliminary estimates of home ranges during brood care were obtained by superimposing a grid on the minimum convex polygon enclosing female locations.

We obtained information on survival of adult females for the period from the time of trapping to the end of radio-tracking, approximately 16 weeks. Poult survival was calculated for the period from the first sighting of the brood to the end of the tracking period, approximately 12 weeks.

RESULTS

The five vegetation associations were classified as follows (González 1992): 40% of total transect in tall forest (not-flooded, ≥30 m height, clear understory), 23% in low palm forest (seasonally flooded, 20 m height, abundant vines, dense understory), 6% in low tinto forest (seasonally flooded, 15 m height, high tree density, small diameter stems), 17% in tall flooded forest (seasonally flooded, ≥30 m height, clear understory), and 14% in secondary forest (not-flooded, 20 m height, dense understory).

From December 1988 through July 1989, 163 transect counts were conducted totaling 274 km. There were no significant differences in numbers of turkeys among transects, vegetation types, or months for the duration of the study (González 1992). However, a tendency towards occurrence in tall and secondary forests was observed (González 1992, González et al. 1996).

In the administrative/tourist area of the park, the number of adult ($D = 0.328$, $P < 0.01$) and juvenile ($D = 0.426$, $P < 0.01$) females decreased significantly in the March nesting period (González 1992). Neither adult nor juvenile male numbers decreased significantly ($P > 0.05$).

During the breeding season, adult male turkeys develop stunning secondary sexual characteristics (González 1992, González et al. 1996). Adult males have a distinctive gobble and courtship display. Gobbles were first heard in early February, reached their peak in March and diminished in May. The gobble begins with several low frequency "thumps", much like the sound of a small gasoline motor starting. As the tempo of thumps increases, the typical gobble is produced.

During the display, males execute an intricate and energetic dance. They begin by tapping their feet at high speed. Then they raise and open their tail feathers in a fan, which they move from side to side. The wings vibrate as they are spread out and down, with the tips barely touching the ground. While the male moves around the female during the dance, he maneuvers his tail feathers so their dorsal surface is constantly visible to the female. Male dances have been observed from 14 February to mid-April.

Mating appears most frequent from 20 March to 10 April, although few copulations have been observed (González et al. 1996). After mating, females begin searching for nesting sites. Nests are built on the ground on

TABLE 1. Nesting, hatching, and adult female and poult survival rates of the Ocellated Turkey in Tikal, Guatemala.

Parameter	1993 (*n*)	1994 (*n*)
Radio-collared females	4	5
Nesting females	3 (75%)	5 (100%)
Females with successful nests[a]	1 (33%)	4 (75%)
Adult female survival	3 (75%)	3 (60%)
Total poults produced	5	22
Surviving poults[b]	0	4 (18%)

[a] Overall female nesting success = 62%.
[b] Overall poult survival rate = 15%.

previously cleared, well-hidden, small depressions. They are usually found in tall grass or brush, although occasionally they are located at the base of trees. Camouflage is the nest's main protection against predators.

Nests had an average of 8.8 ± 2.5 (SE; n = 5) cream-colored eggs mottled with brown. Incubation was 28 days. When hatched, poults are cryptically colored. Hatching (usually occurs) from the end of May to the beginning of July. However, adult females have been observed with poults still with down in September.

Young follow the hen to forest cover as soon as they hatch. This may be to avoid direct sunlight since their plumage appears conspicuous in direct light. Two weeks to a month after chicks begin hatching, females and their broods form groups in which adult females apparently share responsibility for care of the young.

Nine turkeys were captured and fitted with radio transmitters in 1993 and 1994. In March, 1995, five additional females were captured in Tikal. Table 1 shows nesting, hatching, and survival rates for adult females and poults for 1993 and 1994. The survival rate through the breeding period for adult females was 0.75 in 1993 and 0.60 in 1994 (González et al. 1996).

Of the 9 females followed through two nesting seasons, 5 lost their nests to predators. Two of these females renested. Overall, 5 of 8 hens (62%) were successful in nesting and hatching poults. Of the 27 poults produced, 4 survived to the end of the tracking season for a survival rate of 0.15. Of 5 females with broods that were tracked in 1994, 2 died 6 and 15 days after hatching their poults.

Displacement and home ranges were calculated for females captured in 1993 and 1994. The maximum distance between a trapping site and nesting site was 8 km, and the minimum was 0.2 km. The average displacement for 9 nesting attempts was 2.4 km.

The radio-collared females' home ranges averaged 0.28 km^2 (27.6 ha). The female with the largest home range covered approximately 12.5 km^2 (1247.31 ha) with her brood before forming a flock.

Females took their broods under tall forest cover. Of 61 observations of females with young, 87% were in tall forest with non-flooding soils. Analyses of aerial pictures (1:250,000) and cartographic maps (1:50,000) of the surface of Tikal National Park indicate that between 65% and 79% is considered "broadleaf tall forest" (González 1992).

DISCUSSION

Ocellated Turkeys used different vegetation types: open areas or areas with clearings during courting, breeding, and nesting, and tall forest during the rest of the year. This is in contrast to Steadman and coworkers (1979) who reported that *M. ocellata* used the forest for nesting and clearings mainly for feeding.

Habitat use by North American Wild Turkeys (*Meleagris gallopavo*) appears to be similar: forests and small clearings (Bowman et al. 1979, Everett et al. 1979, Campos et al. 1984, Towry et al. 1984, Schemnitz et al. 1985). As with the Ocellated Turkey, adult Wild Turkeys use clearings for their reproductive displays (gobble and strut; Barwick and Speake 1973).

The composition of Ocellated Turkey groups and its variation throughout the year parallels the behavior of the North American Wild Turkey as described by Latham (1976). Selection of nest sites also seems similar. Wild Turkeys will nest in open areas, such as pastures, clearings, scrub, or any type of low vegetation that adequately hides a nest (Cook 1972, Hillestad 1973, Williams et al. 1973, Latham 1976, Anonymous 1979). According to Hillestad (1973), the distance (in a straight line) from the place of mating to the nesting site for *M. gallopavo silvestris* is 2.7 km, similar to the distances between capture and nesting for Ocellated Turkeys in Tikal (2.4 km).

Habitat for broods of the Wild Turkey var-

ies. Some authors (McCabe and Flake 1985, Williams et al. 1973) report that females used forest cover for small chicks. Others have indicated that adequate habitat for poults included clearings and pastures (Hillestad and Speake 1970). Baker and coworkers (1980) found that nearly 50% of their sightings during one brooding period occurred in riparian woodland. Although most of our observations of Ocellated Turkey broods were in tall forest, they probably use other vegetation types and ecotones as they move through their home ranges. Detailed mapping of Tikal's vegetation to determine distribution of specific vegetation types identified in this study is still needed.

The survival rates of Ocellated Turkey females (0.60, 0.75) and poults (0.15) during the breeding season seem to be low. Nesting success for the Ocellated Turkey (62%) is similar to the 59–63% nesting success of Wild Turkeys in southern Florida, where several predator species were present, including skunks, raccoons, and opossums (Williams et al. 1980). According to Hickey (1955, in Williams et al. 1980), this success rate is higher than the overall nesting success of 45% reported for other galliform birds. A relatively high nesting success rate, along with the capacity to renest and the fact that yearling females nest, could partly counteract the low survival rates for hens and poults. Nevertheless, the reproductive success of Ocellated Turkeys in this study is not enough to offset mortality.

The home range calculated for the only female that had a successful brood through the end of a tracking season (12.5 km^2) was eight times as large as the spring and summer ranges of nesting Wild Turkey hens in Alabama (1.49 km^2; Hillestad 1973). Although additional information is necessary to determine the mean and variation in home ranges under differing climatic and vegetation conditions, it seems likely that this species requires large forested areas for successful reproduction.

Our results show that reproductive success of Ocellated Turkeys is low even in the moderately protected conditions within Tikal National Park. This consideration, along with rapid habitat loss and overhunting, indicate that the species could be threatened.

This bird is an important game species in an area where most animal protein is obtained by hunting. At present, prohibitions on hunting would have no effect because Guatemala lacks the necessary means for enforcement. On the basis of the results of this study, the Ocellated Turkey was included in the proposed hunting regulations for the country. The suggested hunting season is from 1 March to 30 May; subsistence hunters have a bag limit of 2 males per week, while sport hunters have a bag limit of 5 males for the season; no hunting of females is allowed. The information provided by radiotelemetry suggests that the hunting season should be shortened to 30–40 days and that the bag limits (for both types of hunters) should be reduced.

Besides hunting regulations and an educational campaign to support them, further research is needed. It is important to determine survival rates year-round and the effects of annual changes in climate, particularly precipitation, on nesting success and poult survival. This information could provide a better estimate of the turnover rate of Ocellated Turkey populations, and therefore provide the basis for adequate management programs.

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AVIAN DIVERSITY IN EL SALVADOR

OLIVER KOMAR[1,2]

ABSTRACT.—Recent field studies have revealed many species of birds new for El Salvador suggesting that the country's few protected areas may be especially important for conserving regional biodiversity. Seventeen percent of the landscape or 359,000 ha is covered with natural forest or scrub habitats, of which 38,000 ha are coastal mangrove forests. An additional 196,000 ha (9% of El Salvador) are coffee plantations, a forest-like habitat used by many birds. Of 508 bird species known to occur in the country, 310 are breeding residents; the others are migratory visitors, transients, or vagrants. Seventeen species occurring in El Salvador are endemic to the highlands of northern Central America and one species is endemic to the Pacific slope lowlands of northern Central America. About 270 species are habitat specialists with highly restricted ranges within El Salvador. In all, 254 species (>50% of the avifauna) are threatened by habitat loss, pollution, hunting, and exploitation for the pet trade. Of these, 117 are in danger of extinction at the national level and three are believed already extirpated. Much additional field work is needed to understand the status and abundance of El Salvador's birds. This report includes a complete list of reported species with classification of residency status, threatened status, and distribution. This list can serve as a resource for interpreting field observations produced by environmental impact studies or conservation projects in El Salvador. A second list includes 73 species that probably occur in El Salvador but have not been reported.

El Salvador is a small nation (20,746 km^2) confined to the Pacific slope of northern Central America (Fig. 1). Unlike nearby Belize, which is virtually the same size, but mostly unpopulated and about 75% forested, El Salvador is only about 18% forested (including scrub habitats) and has the densest human population in Latin America. The 1992 population was 5.12 million, increasing 1.42% annually (Dirección General de Estadística y Censos 1995). Biological collectors and tropical ecologists, attracted to countries with extensive wild areas, have largely avoided El Salvador. Only a few museum expeditions (Miller 1932, Dickey and van Rossem 1938, Marshall 1943, Burt and Stirton 1961) have visited the country. Given this minimal international interest, local biological expertise has been even slower to develop. The not surprising result is the ubiquitous perception that El Salvador is depauperate in biodiversity. No scientific study has established an overall lack of biodiversity, however. Recent studies of trees (Berendsohn 1995) and birds (Thurber et al. 1987, West 1988, present study) have discovered so many unrecorded species that the old perception must be thrown out. In the nearby Pacific slope highlands of western Guatemala, Vannini (1994) reported the "second richest avian province in northern Central America," supporting the assertion that the Pacific slope of northern Central America is rich in biodiversiy.

Biodiversity is generally related to diversity of habitats, which in turn is often related to altitudinal range (Hamilton et al. 1964, Johnson 1975). El Salvador has a diverse mosaic of habitats, caused in part by the volcanic geography of the region and an altitudinal range 0–2730 m. On the Pacific coastal plain, there are swamp forests (now very restricted), humid and dry tropical forests, mangrove swamps and estuaries, and freshwater lagoons. Rich offshore waters attract pelagic seabirds. Just inland is a chain of young volcanoes ranging up to 2365 m, which features an extensive cloud forest on the Santa Ana Volcano. The dry central valley provides additional lowland habitats and to the north, the foothills of the geologically ancient Central American mountains (the "cordillera") provide pine and oak-pine forests. The higher points along the Honduras border, such as at Montecristo National Park and El Pital (elev. 2730 m) feature habitat for numerous cloud forest species.

Van Rossem reported 380 species, or 75% of the birds now known from El Salvador, when he collected widely in the country in 1912 and 1925–1927 (Dickey and van Rossem 1938). A few additional species were reported by Marshall (1943). Thurber and co-

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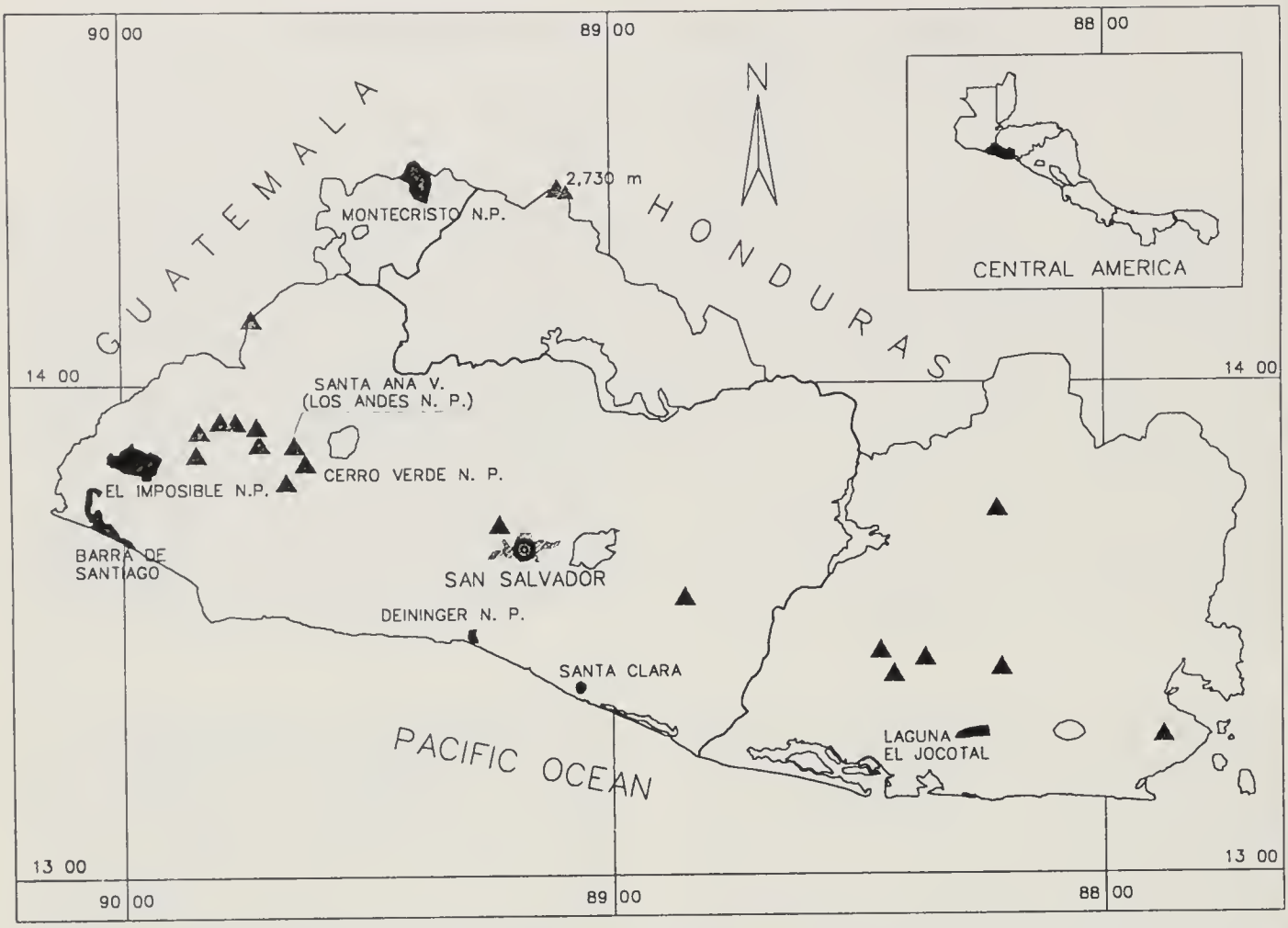

FIG. 1. Protected areas and geographical features of El Salvador. The insert shows El Salvador's position within Central America. (Prepared by Alvaro Moisés-Calderón, based on Reyna de Aguilar et al. 1996.)

workers (1987) added 60 species to the list, summarizing most of the ornithological activity in El Salvador through 1980. That report incorporated unpublished observations from Juan Antonio Gómez, Russell Greenberg, Peter Hamel, Burt Monroe, Larry Naylor, and Jane West (see West 1988), and reviewed new records published in short notes and other relatively obscure sources (e.g., Dickerman 1972, Feduccia 1976, Hellebuyck 1983). One source for pelagic records (Jehl 1974) was not reviewed by Thurber and coworkers (1987). Little new information was added during the El Salvadoran civil war from 1980 to 1992.

Between 1992 and 1996, I spent 22 months studying El Salvador's birds, and have observed 22 species not previously reported (details of documentation for these species have been or will be reported separately, e.g., Komar and Rodríguez 1995). During this same period, Salvadoran aficionados and biologists (Alfredo Chahín, Juan Pablo Domínguez, Alvaro Moisés, Fabricio Pérez, Karla Pérez; pers. comm.) have reported seven additional species. Three more species not reported elsewhere were collected by the El Salvador Museum of Natural History in the 1970s and 1980s (Figueroa de Tobar 1993).

My objectives in this paper are to review all bird species known to occur in El Salvador by habitat and altitudinal distribution, migratory/resident status, and endemism; and to review endangered and threatened species, conservation effort, and future ornithological studies.

METHODS

Residency status classifications.—A species was classified as "breeding" if observers have noted nest building or the presence of juveniles too young to have completed the post-juvenal molt. Resident or non-migratory species not observed breeding were classified "status uncertain." "Migrants" were species that spend part of each year in El Salvador, generally remaining in El Salvador for an extended period (several months) before returning to their country of origin. The majority of migratory species breed in North

America and spend the northern winter in El Salvador. I classified some migratory species as "transients" if they were not known to winter in El Salvador regularly. Migratory species with both breeding and nonbreeding populations in El Salvador were listed as both breeding and "partial migrants." For at least one species in this category, the Blue Grosbeak (*Guiraca caerulea*), the breeding population may migrate south during the nonbreeding season. Other migratory species that typically can be found all year in El Salvador but are not known to breed were also "partial migrants." Species that breed in El Salvador and then migrate to South America were "breeding visitors."

A species was "vagrant" or "casual" if breeding had not been observed and there were fewer than five reports. A species was "hypothetical" if reported by a reliable observer but without photographic, audiotape, or specimen evidence. New photographic and audiotape documentation was accepted when confirmed directly by the author. I did not review museum collections to confirm specimen documentation reported in the literature.

I followed Bibby and coworkers (1992) in defining "endemic" species as those with breeding distributions smaller than 50,000 km^2; thus most species restricted to northern Central America are endemic. When possible, I indicated the presence of endemic subspecies. However, I have not exhaustively analyzed the literature on subspecies and many more recognized subspecies than I have indicated may actually be endemic. I have only indicated endemic subspecies for species restricted to the highlands (Komar 1994).

Criteria for threatened status.—Most threatened species are habitat specialists subject to decline after major habitat loss. Threatened species also experience exceptional human pressure for reasons that include the cage bird trade and poisoning from pesticides. The former applies to parrots, parakeets, owls, toucans, and buntings. The latter applies to hawks, falcons, and owls which may also be killed for superstitious reasons. These species have decreased in suitable habitats throughout the country (Thurber et al. 1987). Species classified as "in danger" are especially vulnerable. They are either (1) reduced to one or two small populations or (2) more widely distributed but present in very low numbers. The El Salvador populations for most endangered species is under 400 individuals and for many species is much lower (see Discussion). Species that have only been reported casually (<5 records) were not considered as threatened or in danger because they may not be part of the regular Salvadoran avifauna. As these species become recognized as resident or part of the regular avifauna, their threatened status should be reevaluated.

Distribution and habitat use classification.—I classified each species as either an altitudinal generalist or highlands or lowlands specialist, and as either an open habitat generalist or specialist, forest generalist or specialist, or aquatic habitat specialist. Lowland specialists are found mostly below 1000 m elevation; highland specialists mostly above 1000 m. I considered scrub or matorral habitats as open habitats, not forest habitats. I did not distinguish between salt and fresh water habitats because only a few marine species are restricted to salt water habitats. There are virtually no salt marshes in El Salvador, and thus no species specializing in salt marsh habitats.

Species restricted geographically were designated as either west, east, north, or coastal. Species limited to the west are found in the western third of the country, with San Salvador as the easternmost limit of distribution. Species limited to the north are found in the cordillera near the Honduran border. Species limited to the east are found in the eastern third of the country. Coastal species are limited to estuaries, beaches, and marine waters. A species may fall into three or more of these above categories.

Information about habitat use and distribution for some rare or poorly known species in El Salvador was speculated with the hope that the publication of the present analysis will stimulate field workers to publish their own observations so that the information can be corrected.

I derived the list of predicted species in Appendix 2 based on the distribution maps in Howell and Webb (1995). All species listed were shown in the guide as occurring in El Salvador or close to its borders. The taxonomy used for both appendices follows the American Ornithologists' Union (1998).

RESULTS

Despite the high level of deforestation, economic dependence on agriculture, and abundant human presence in virtually all corners of the country, 508 species of birds have been reliably reported from El Salvador (Appendix 1). An additional 73 species are expected to occur in El Salvador (Appendix 2). Belize, with its extensive wilderness and long history of ecological studies and intense nature observation by visiting scientists, has a bird list of 543 species (Miller and Miller 1995). With continued field studies, we may find that El Salvador has more species than Belize.

I have relegated four species previously reported as occurring in El Salvador to Appendix 2 because of lack of a primary source or because recent changes in the political border with Honduras make some collection localities questionable, especially for birds documented from Sabanetas by Thurber and coworkers (1987). Parker and coworkers (1996) listed the Flammulated Owl (*Otus flammeolus*) for El Salvador but I have not found a primary source. Birds known in El Salvador only from Sabanetas (now in Honduras) include Mountain Trogon (*Trogon mexicanus*),

TABLE 1. Status of birds reported in El Salvador.

	No. of documented species	No. of hypothetical species	Total no. of species
Breeding, non-migratory residents	197	0	197
Breeding, partially-migratory residents	34[a]	0	34
Breeding visitors	3	0	3
Breeding suspected (status uncertain)	74[a]	2	76
Subtotal for breeding species	308	2	310
Non-breeding visitor	110[b]	4	114
Transient	16	0	16
Migratory vagrant (status uncertain)	27	21	48[c]
Non-migratory vagrant (status uncertain)	12	8	20
Subtotal for non-breeding species	165	33	198
Grand total			508

[a] Five documented partially-migratory residents have not actually been confirmed as breeding. These are Turkey Vulture, Sharp-shinned Hawk, Zone-tailed Hawk, Collared Plover, and Blue-headed Vireo.

[b] At least five documented winter visitors are actually far more abundant as transients: Swainson's Hawk, Merlin, Franklin's Gull, Sabine's Gull, and Kentucky Warbler.

[c] Includes at least 22 probable transients (10 documented and 12 hypothetical) recorded only once or twice, and other species that may be irregular winter visitors.

Sedge Wren (*Cistothorus platensis*), and Brown Creeper (*Certhia americana*).

Status classification.—Breeding has been documented for 229 species, although 310 species probably breed in El Salvador (Table 1). Three breeding visitors, Plumbeous Kite (*Ictinia plumbea*), Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*), and Yellow-green Vireo (*Vireo flavoviridis*), spend the winter in South America. Populations of at least 34 resident species are augmented by migratory populations during the northern winter. Apparent "vagrants" of 21 non-migratory species may represent additional breeding residents.

El Salvador provides wintering habitat to at least 114 non-breeding visitors (plus the 34 partially migratory species mentioned above). Many of the 48 migratory vagrants recorded may also be regular winter visitors. Sixteen species are primarily transients in El Salvador, rarely spending a winter or summer. Of the 48 migratory vagrants in Table 1, 22 are probably regular transients in El Salvador, making a total of 38 transient species.

Northern Central America is a center for avian endemism (Bibby et al. 1992), with 18 El Salvador species geographically restricted to northern Central America between the Isthmus of Tehuantepec and the Nicaraguan Depression. Highland habitats are especially important for these endemic species. Of the 18 endemics, 17 are most abundant in the highlands and only one is restricted to the lowlands. Several species are restricted to the Pacific slope of northern Central America, including the White-bellied Chachalaca (*Ortalis leucogastra*), Rufous Sabrewing (*Campylopterus rufus*), White-eared Ground Sparrow (*Melozone leucotis*), and Bar-winged Oriole (*Icterus maculialatus*). More than 75 endemic subspecies of highland-restricted birds occur in El Salvador.

At least 254 bird species, or more than 50% of the known avifauna, are threatened with extinction in El Salvador and 117 of these species are now so restricted in range or population that I consider them in danger (Appendix 1). Three other species recorded this century, the Jabiru (*Jabiru mycteria*), Ornate Hawk-Eagle (*Spizaetus ornatus*), and Scarlet Macaw (*Ara macao*), may in fact now be extirpated, although natural recolonization is possible in the future. No data exist for species extirpated prior to this century.

Diverse natural habitats.—The remnant patches of natural habitat in El Salvador indicate the natural diversity characteristic of the region. The country is geographically and geologically diverse, with both old and new mountain ranges, numerous volcanic formations, and altitudes reaching over 2000 m above sea level in four different parts of the country. Holdridge (1975) described six prin-

TABLE 2. Land use in El Salvador.[a]

Land use type	Area (ha)	% of national terrain
Non-permanent farming[b]	1,389,778	66.2
Permanent crops		
Coffee plantations	195,709	9.3
Coconut plantations	1314	0.1
Tree plantations[c]	6584	0.3
Natural forests (other than mangrove) and scrub	320,442	15.3
Mangrove forests	38,344	1.8
Lava flows	9398	0.4
Bodies of water	35,187	1.7
Urban and developed areas	67,910	3.2

[a] Source: Dirección General de Economía Agropecuaria (1996).
[b] Includes corn, beans, grazing, sugar cane, rice, and miscellaneous crops.
[c] Source: Cruz Rodríguez and Gómez Vaquerano (1996).

TABLE 3. Distribution of habitat specialist bird species (recorded at least five times) in El Salvador.

Species restricted to:	Breeding/ uncertain	Non-breeding
Forests		
No altitude restriction	8	0
Highland	73	2
Lowland	47	4
Forests subtotal	128	6
Non-forests		
No altitude restriction	2	1
Highland	15	0
Lowland	21	9
Aquatic habitats	38	56
Non-forests subtotal	75	67
Total	191	72

cipal life zones in the country. Recent data on the quantity of natural habitat in El Salvador (Table 2) indicate that 358,786 ha, or 17.3% of the national territory, is presently covered by mangrove forest, natural forest or shrubs. However, more than half of this area is young secondary forest, and may soon be converted into agricultural land. An additional 203,607 ha are permanent crops (coffee, coconut, tree plantations) that provide cover and feeding habitats for birds, and 9400 ha are recent lava flows that may eventually provide vegetation cover.

The presence of a large variety of natural habitat types has permitted the survival, albeit tentative, of many avian species that are habitat specialists. These species have small, patchy distributions and often are present in low numbers. For example, 23 bird species' Salvadoran ranges are mostly restricted to 5000 ha in the El Imposible National Park (Komar and Herrera 1995a). Habitat specialist species are concentrated in forest habitats, especially in the highlands, and in wetlands (Table 3). The majority of the wetland specialists are migratory aquatic species. Wetlands are relatively rare in El Salvador, occupying only 35,187 ha (Table 2).

Habitat use and distribution.—Of the 310 resident and suspected breeding species, 125 are forest specialists, 67 are forest generalists, 39 are open specialists, 61 are open generalists, and 38 live mainly in aquatic habitats (several species are counted in more than one category; Appendix 1). These figures highlight the importance of forests for avian biodiversity in El Salvador.

A breakdown of altitudinal distributions of El Salvador's 282 resident, non-aquatic species indicates the importance of the country's highlands for the conservation of its avian biodiversity. Even though only about 20% of the country has an elevation greater than 1000 m, 104 species (about 20%) are restricted to these highlands. In all, 133 species are restricted to lowlands and 45 are altitudinal generalists. Thus the density of altitudinally restricted species is much greater in the highlands than in the lowlands. Expanding the analysis to all 398 species classified for altitude preference (aquatic species excluded), 191 prefer lowlands, 75 are altitudinal generalists, and 133 prefer highlands.

Despite El Salvador's small size, more than 100 bird species are restricted to geographical areas representing less than one third of the nation. The western third of the country appears to have more diverse bird populations than the central and eastern thirds, with 41 species (plus 3 vagrants) reported only from the west (mostly at El Imposible National Park and Santa Ana Volcano). Six species plus one vagrant are restricted to the eastern third of the country. Indeed, most of the birds restricted to the north and to the coast also occur in the western third of the country. Dividing the country in latitudinal thirds, the northern third is more diverse than the central and

southern (coastal) thirds. Restricted to the north, such as at Montecristo National Park, are 41 residents or regular visitors, plus 7 vagrant species. Thirty species, plus 16 vagrant species, are restricted to the coast or marine waters.

DISCUSSION

Characterizing the biodiversity of a country is not a simple task. Ideally one should describe the diversity of ecosystems, species, and populations (subspecies or other genetically isolated groups), as well as some measure of abundance for each of these entities. Most biodiversity studies develop an index that combines species richness with evenness of abundance (Primack 1993). Since the goal of the present paper was not to compare El Salvador's biodiversity with that of other regions, preparing such an index was not necessary. Also, for the overall characterization, it was hardly possible to analyze evenness of abundance, given the paucity of studies of avian abundance in specific habitat types. Only three studies of forest bird communities in El Salvador have determined a relative abundance index (Komar and Herrera 1995a, b; Komar 1996).

Considering only the number of species present in a region as indicative of its biodiversity value would be misleading. For example, migration monitoring at oceanic islands typically records numerous vagrants wandering off course (e.g., Lynch and Johnson 1974), which may not survive after making landfall on the islands. Thus considering vagrants as part of a site's biodiversity value is unwarranted. I suggest that the presence of breeding species is the most important measure of avian diversity, followed by nonbreeding visitors that return to the area as part of their annual cycles. Less important are migratory transients on their way to other areas. Finally, accidental vagrants whose survival is doubtful and whose presence is due to chance and not to the natural attractiveness of local habitats, have little relevance to measures of biodiversity.

Much more field work will be needed to determine the actual number of breeding residents in El Salvador. The possibility exists that some of the 77 non-migratory species recorded as "breeding suspected" in Table 1, such as Black-crowned Night-Heron (*Nycticorax nycticorax*), Hook-billed Kite (*Chondrohierax uncinatus*), Lesser Swallow-tailed Swift (*Panyptila cayennensis*), and Eastern Meadowlark (*Sturnella magna*) are in fact dispersers from breeding populations in neighboring countries and not part of the regular breeding avifaunal community. Some of these species may be migratory visitors, although migration has not been documented for many of them. Little is known about "intratropical" bird migrations. For example, it is not known to what extent northern migrants supplement El Salvador's resident populations of Red-billed Pigeon (*Columba flavirostris*), Green-breasted Mango (*Anthracothorax prevostii*), Tropical Pewee (*Contopus cinereus*), Clay-colored Robin (*Turdus grayi*), and Red-legged Honeycreeper (*Cyanerpes cyaneus*), all of which have been reported to migrate (Dickey and van Rossem 1938, Thiollay 1977, Howell and Webb 1995). Among the winter visitors to El Salvador is the "Red-throated" Green Parakeet (*Aratinga holochlora rubritorques*) which is reported to migrate from nearby Guatemala and Honduras (Howell and Webb 1995).

In most of El Salvador, where the terrain is cultivated with grains, coffee, sugar cane, or used for pasture (Table 2), species richness is generally low and species tend to be either abundant or rare (this lack of evenness in abundance indicates low diversity). In many areas, low maintenance fincas (farms) with abundant fruit trees or small tree plantations help maintain biodiversity (Thiollay 1995) and serve as biological corridors. One of the principal agricultural crops, coffee, is grown on 9.3% of the national terrain; when managed with traditional shade practices, this agricultural habitat serves moderately well to preserve avian biodiversity. Coffee fincas suit many generalist species, including a large array of Nearctic-Neotropical migratory birds, because of the permanent nature of the crop and the presence of shade trees in most plantations (Vannini 1994). However, Salvadoran plantations often utilize a near monoculture of shade trees (*Inga* spp.), greatly simplifying the structure of the plantations, and limiting the biodiversity within them. Nonetheless, some common birds in coffee plantations would probably disappear if these plantations were

converted to non-permanent crops or to residential and industrial developments.

The principal sanctuaries for El Salvador's still rich biodiversity are the small patches of forest and other natural habitats. Most of these areas are secondary forest; sometimes successional areas only a few years old. Extensive areas of agricultural land in the eastern part of the country were abandoned during the recent civil war (1980–1992) and now appear as scrubby secondary forest. El Salvador still has some areas with climax or old primary forest, such as occur in deep ravines of El Imposible National Park, on the inner slopes of the Coatepeque Caldera (San Marcelino Wildlife Refuge), and on high mountain peaks, such as Santa Ana Volcano (Los Andes National Park) and in Montecristo National Park.

The presence of many endemic species and subspecies of birds in El Salvador suggests that studies of other taxa will also encounter high endemism (Bibby et al. 1992). Isolation of natural habitat patches on volcanoes and mountain ranges in El Salvador has permitted the evolution of at least five bird subspecies completely restricted to El Salvador (Komar 1994) and unknown numbers of endemic plant and animal species. Thus El Salvador may play an important role in the conservation of the region's biodiversity. It is imperative that the natural habitats in El Salvador receive conservation protection and that Salvadoran land managers be well-informed of the importance of their stewardship for the conservation of biodiversity.

Endangered species.—Only one species of bird reported from El Salvador, the Golden-cheeked Warbler (*Dendroica chrysoparia*), is listed as globally threatened (in danger of extinction) by Wege and Long (1995). However, many Salvadorans recognize the importance of protecting their natural heritage for national reasons and do not focus so much on global priorities. Most Salvadoran people and the Salvadoran government accept the problem of Salvadoran species "on the route to extinction" in their country. Therefore, I have analyzed threatened status at the national level. Furthermore, bird population studies and taxonomic works in Latin America are sufficiently scarce that ornithologists can not yet determine with precision which are the globally threatened species in the region. Many endemic populations classified by 19th-century taxonomists as subspecies of wide-ranging forms may qualify as species by today's standards (Peterson et al. 1998) and, because of their restricted ranges, may be globally threatened.

For the first time, we now have a list of threatened Salvadoran birds (Appendix I) for which all bird families were considered based on criteria. An earlier list of threatened species only considered non-Passeriformes (Juárez and Alcides Orellana 1985) and neither that list nor another attempt (Thurber et al. 1987) presented criteria for selection. Some of the endangered species in El Salvador are still locally common in appropriate habitats, but most are generally uncommon or rare within their often restricted habitats.

Most of the 117 nationally-endangered species have small populations of under 400 individuals within El Salvador. Some endangered species have larger populations, such as the White-fronted Parrot (*Amazona albifrons*) and the Emerald Toucanet (*Aulachorynchus prasinus*), but are nevertheless subject to severe population pressure from the pet trade or loss of habitat. One species I consider endangered, the Rufous-browed Wren (*Troglodytes rufociliatus*), numbers over 4000 individuals but may be restricted in El Salvador to just one 600 ha forest patch on the Santa Ana volcano, where it is the most abundant species (unpubl. data). One casual species that may not be part of the regular Salvadoran avifauna, the Golden-cheeked Warbler, was listed as endangered because it is internationally recognized as endangered (Wege and Long 1995), but other species with fewer than 5 records have not been classified as endangered because they do not appear to be regular parts of the El Salvador avifauna.

Wildlife conservation in El Salvador.—Wildlife and habitat conservation is a recent phenomenon in El Salvador; the first national park, Montecristo, was established in 1987 (although the park service was established in 1974). The current protected area system includes eight areas and 10,919 ha, or 0.5% of the country, managed under the authority of either the Salvadoran National Parks and Wildlife Service (in some cases in collaboration with non-governmental organizations) or the Salvadoran Institute for Tourism. Reyna de Aguilar and coworkers (1996) proposed in-

creasing the protected areas to 49,236 ha (2.37% of El Salvador), to encompass 24 conservation areas as part of a Minimum System of Protected Areas. Given the presence of natural vegetation cover of 13–18% of the country, conservation efforts should be expanded further.

One of the largest problems facing wildife conservationists in El Salvador is uncertainty about where wildlife habitat currently exists. A detailed and accurate habitat map does not exist and recent estimates of El Salvador's forest cover vary widely. Zambrano (1996) estimated current forest cover by applying a deforestation rate of 4500 ha per year to data on forest cover in 1975 and then added an estimate for second growth generated in farming areas abandoned during the recent war. His total estimate of 18.1% of the country is close to the data reported in Table 2 (17.3%). Cruz Rodríguez and Gómez Vaquerano (1996) concluded that only 12% of El Salvador was forested and Reyna de Aguilar and coworkers (1996) reported 13% forest and shrub cover, citing Dirección General de Recursos Naturales Renovables (1981).

As an indication of the precarious existance of the threatened forest-specialist birds in El Salvador, Zambrano (1996) predicted that all 34,298 ha of extant primary forest will be destroyed by the year 2001 should current rates of forest loss continue. Laws and park protection plans exist to prevent such a disaster.

Directions for future ornithological studies.—Compared to political states of comparable size, such as Belize or Massachusetts, El Salvador's ornithology remains poorly known. Relative abundance information for birds is not available for the majority of habitats, or even protected areas such as Montecristo National Park, which contains El Salvador's largest cloud forest. The highest priority should be to inventory (including analysis of relative abundance) avian diversity in every major habitat type in El Salvador, not just within the currently protected areas. Primary habitats should be assesed first. Relative abundance data are important for revealing which habitats are critical for survival of a species. For example, the endemic and endangered Bar-winged Oriole is common in at least one mid-elevation, humid evergreen forest in the Lake Coatepeque caldera but uncommon in coffee plantations (where breeding is not documented). Without the forest it will likely become extinct. Without the relative abundance information, conservationists might have thought that conserving shade coffee plantations would be sufficient for the survival of the oriole. Conservation activists need comprehensive surveys in order to identify critical habitats and specific sites for conservation of bird species (see Stotz et al. 1996, for an excellent discussion on deriving conservation priorities). Salvadoran biologists and ornithologists should begin to plan such projects.

Avian densities or relative abundances must be calculated during both the breeding and non-breeding seasons. The latter season is when the avian communities are augmented by the arrival of Nearctic-Neotropical migrants. Taxonomic work, including some scientific collecting, is also necessary to establish which species live in El Salvador. These future inventories represent a huge amount of work for Salvadoran ornithologists. Life history and ecological studies are needed to determine the survival needs of endangered and threatened species. Populations of the 190 vulnerable habitat-specialist resident species should be monitored over the long-term (multiple years), with companion studies of breeding productivity and survivorship. Another major task and critical step for bird conservationists will be to determine the exact distribution and amount of each natural habitat type and then arrange for the permanent protection of these lands.

In summary, there is a great need for continued and expanded ornithological studies in El Salvador. If funding were available, many ornithologists could be kept busy for many years. In reality, professional Salvadoran ornithologists number fewer than six, and none are employed regularly to study birds. Nonetheless, abundant human resources, widespread interest in wildlife conservation among the educated sector of El Salvador, and the present relatively strong financial support for environmental projects suggest the possibility of increased training opportunities for biology students, and for encouraging numerous ornithological field studies. Birds are the most visible and attractive component of El Salvador's faunal biodiversity; the study and promotion of the country's avian treasures, such

as its national bird the Turquoise-browed Motmot (*Eumomota superciliosa*), are keys to the future preservation of El Salvador's biodiversity, natural resources, and environment.

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APPENDIX I. Status and distribution of all documented and hypothetical bird species observed in El Salvador.[a]

Family English name	Scientific name	Status	Distribution
TINAMIDAE			
Thicket Tinamou	*Crypturellus cinnamomeus*	B, d	FG, L
PODICIPEDIDAE			
Least Grebe	*Tachybaptus dominicus*	B, d	W
Pied-billed Grebe	*Podilymbus podiceps*	B, d	W
Eared Grebe	*Podiceps nigricollis*	M, d	W
PROCELLARIIDAE			
Wedge-tailed Shearwater	*Puffinus pacificus*	T, H, C(2)	W, c
Audubon's Shearwater	*Puffinus lherminieri*	T, H, C(2)	W, c
HYDROBATIDAE			
Black Storm-Petrel	*Oceanodroma melania*	M, H	W, c
PHAETHONTIDAE			
Red-billed Tropicbird	*Phaethon aethereus*	VU, C(2), H	W, c
SULIDAE			
Masked Booby	*Sula dactylatra*	T	W, c
Blue-footed Booby	*Sula nebouxii*	T, H, C(2)	W, c
Brown Booby	*Sula leucogaster*	MP	W, c
Red-footed Booby	*Sula sula*	T, H, C(2)	W, c
PELECANIDAE			
American White Pelican	*Pelecanus erythrorhynchus*	M, d	W
Brown Pelican	*Pelecanus occidentalis*	MP	W, c
PHALACROCORACIDAE			
Neotropic Cormorant	*Phalacrocorax brasilianus*	B, D	W
ANHINGIDAE			
Anhinga	*Anhinga anhinga*	B, D	W
FREGATIDAE			
Magnificent Frigatebird	*Fregata magnificens*	MP	W
ARDEIDAE			
Pinnated Bittern	*Botaurus pinnatus*	VU, C(4)	W, e
American Bittern	*Botaurus lentiginosus*	M, d	W, e
Least Bittern	*Ixobrychus exilis*	B, D	W
Bare-throated Tiger-Heron	*Tigrisoma mexicanum*	B, D	W
Great Blue Heron	*Ardea herodias*	M, d	W
Great Egret	*Ardea alba*	B, MP, d	W
Snowy Egret	*Egretta thula*	B, MP, d	W
Little Blue Heron	*Egretta caerulea*	MP	W
Tricolored Heron	*Egretta tricolor*	B, MP, d	W
Reddish Egret	*Egretta rufescens*	MP, d	W, c
Cattle Egret	*Bubulcus ibis*	B	W
Green Heron	*Butorides virescens*	B, MP	W
Agami Heron	*Agamia agami*	VU, C(1), H	W
Black-crowned Night-Heron	*Nycticorax nycticorax*	U, d	W
Yellow-crowned Night-Heron	*Nyctinassa violacea*	B, MP, d	W
Boat-billed Heron	*Cochlearius cochlearius*	B, D	W
THRESKIORNITHIDAE			
White Ibis	*Eudocimus albus*	B, MP, d	W
White-faced Ibis	*Plegadis chihi*	VM, C(2)	W
Roseate Spoonbill	*Ajaia ajaja*	MP, D	W

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
CICONIIDAE			
Jabiru	*Jabiru mycteria*	VU, C(2+), X	W
Wood Stork	*Mycteria americana*	MP, d	W
CATHARTIDAE			
Black Vulture	*Coragyps atratus*	B	OG, AG
Turkey Vulture	*Cathartes aura*	U, MP	OG, AG
Lesser Yellow-headed Vulture	*Cathartes burrovianus*	VU, C(2), H	OS, L, w
King Vulture	*Sarcoramphus papa*	B, D	FG, AG, w
ANATIDAE			
Black-bellied Whistling-Duck	*Dendrocygna autumnalis*	B	W
Fulvous Whistling-Duck	*Dendrocygna bicolor*	B, d	W
Snow Goose	*Chen caerulescens*	VM, C(1), H	W, OS, L
Muscovy Duck	*Cairina moschata*	B, D	W
American Wigeon	*Anas americana*	M, d	W
Blue-winged Teal	*Anas discors*	M	W
Northern Shoveler	*Anas clypeata*	M, d	W
Northern Pintail	*Anas acuta*	M, d	W
Green-winged Teal	*Anas crecca*	M, d	W
Lesser Scaup	*Aythya affinis*	M, d	W
Masked Duck	*Nomonyx dominicus*	B, D	W
Ruddy Duck	*Oxyura jamaicensis*	U, MP, d	W
ACCIPITRIDAE			
Osprey	*Pandion haliaetus*	MP, d	W
Gray-headed Kite	*Leptodon cayanensis*	B, D	FS, L
Hook-billed Kite	*Chondrohierax uncinatus*	U, D	FG, AG
Swallow-tailed Kite	*Elanoides forficatus*	T, C(1), H	FG, L
White-tailed Kite	*Elanus leucurus*	B	OG, L
Snail Kite	*Rostrhamus sociabilis*	VU, C(3)	W, OS, L
Double-toothed Kite	*Harpagus bidentatus*	VU, C(3)	FG, AG
Mississippi Kite	*Ictinia mississippiensis*	T, C(1), H	FG, AG
Plumbeous Kite	*Ictinia plumbea*	BM, D	FS, L
Black-collared Hawk	*Busarellus nigricollis*	B, D	W, FS, L
Northern Harrier	*Circus cyaneus*	M, d	OG, L
Sharp-shinned Hawk	*Accipiter striatus*	M	OG, FG, AG
	Accipiter striatus chionogaster	U, EE, d	H
Cooper's Hawk	*Accipiter cooperi*	M, H, d	FG, AG
Crane Hawk	*Geranospiza caerulescens*	U, D	FG, L
White Hawk	*Leucopternis albicollis*	B, D	FS, L, w
Gray Hawk	*Asturina nitida*	B, d	FG, L
Common Black-Hawk	*Buteogallus anthracinus*	B, d	FG, L
Mangrove Black-Hawk	*Buteogallus subtilis*	B, d	FS, L
Great Black-Hawk	*Buteogallus urubitinga*	B, D	FG, L
Harris's Hawk	*Parabuteo unicinctus*	U, D	OS, L
Solitary Eagle	*Harpyhaliaetus solitarius*	VU, C(1), H	FG, H, n
Roadside Hawk	*Buteo magnirostris*	B, d	OG, L
Broad-winged Hawk	*Buteo platypterus*	M, d	FG, H
Short-tailed Hawk	*Buteo brachyurus*	U, d	FG, AG
Swainson's Hawk	*Buteo swainsoni*	T, M	OG, L
White-tailed Hawk	*Buteo albicaudatus*	U, D	OG, L
Zone-tailed Hawk	*Buteo albonotatus*	U, MP	OG, L
Red-tailed Hawk	*Buteo jamaicensis*	B, MP, EE, d	FG, H
Black Hawk-Eagle	*Spizaetus tyrannus*	B, D	FS, AG, w
Ornate Hawk-Eagle	*Spizaetus ornatus*	U, X	FS, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
FALCONIDAE			
Barred Forest-Falcon	*Micrastur ruficollis*	U, D	FS, AG
Collared Forest-Falcon	*Micrastur semitorquatus*	B, D	FG, L
Crested Caracara	*Caracara plancus*	B, d	OG, L
Laughing Falcon	*Herpetotheres cachinnans*	B, d	FG, L
American Kestrel	*Falco sparverius*	MP	OG, AG
	Falco sparverius tropicalis	B, EE	H
Merlin	*Falco columbarius*	T, M	OG, L
Bat Falcon	*Falco rufigularis*	B, D	OS, L
Peregrine Falcon	*Falco peregrinus*	M, d	OS, L
CRACIDAE			
White-bellied Chachalaca	*Ortalis leucogastra*	B, E, d	FG, L
Crested Guan	*Penelope purpurescens*	B, D	FS, L, w
Highland Guan	*Penelopina nigra*	B, E, D	FS, H, w
Great Curassow	*Crax rubra*	B, D	FS, L, w
ODONTOPHORIDAE			
Buffy-crowned Wood-Partridge	*Dendrortyx leucophrys*	B, EE, d	FG, H
Singing Quail	*Dactylortyx thoracicus*	U, EE(3), d	FS, H
Ocellated Quail	*Cyrtonyx ocellatus*	U, E, D	FS, H, n
Crested Bobwhite	*Colinus cristatus*	B	OG, L
RALLIDAE			
Ruddy Crake	*Laterallus ruber*	B, d	W
Rufous-necked Wood-Rail	*Aramides axillaris*	B, D	FS, AG, w
Gray-necked Wood-Rail	*Aramides cajanea*	U, D	FS, L, w
Sora	*Porzana carolina*	M, d	W
Yellow-breasted Crake	*Porzana flaviventer*	B, D	W, e
Spotted Rail	*Pardirallus maculatus*	VU, C(2)	W
Purple Gallinule	*Porphyrula martinica*	B, d	W
Common Moorhen	*Gallinula chloropus*	B, MP, d	W
American Coot	*Fulica americana*	B, MP, d	W
ARAMIDAE			
Limpkin	*Aramus guarauna*	B, D	W
BURHINIDAE			
Double-striped Thick-knee	*Burhinus bistriatus*	B, D	OS, L, e
CHARADRIIDAE			
Black-bellied Plover	*Pluvialis squatarola*	MP	W, c
American Golden-Plover	*Pluvialis dominica*	T	W, OS, L
Collared Plover	*Charadrius collaris*	U, MP	W, c
Snowy Plover	*Charadrius alexandrinus*	M, D	W, OS, L, c
Wilson's Plover	*Charadrius wilsonia*	B, MP, d	W, OS, L, c
Semipalmated Plover	*Charadrius semipalmatus*	MP	W
Killdeer	*Charadrius vociferus*	M	W, OS, L
HAEMATOPODIDAE			
American Oystercatcher	*Haematopus palliatus*	B, D	W, OS, L, c
RECURVIROSTRIDAE			
Black-necked Stilt	*Himantopus mexicanus*	B, MP, d	W, OS, L
American Avocet	*Recurvirostra americana*	M	W
JACANIDAE			
Northern Jacana	*Jacana spinosa*	B	W, OS, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
SCOLOPACIDAE			
Greater Yellowlegs	*Tringa melanoleuca*	M	W
Lesser Yellowlegs	*Tringa flavipes*	M	W
Solitary Sandpiper	*Tringa solitaria*	M	W
Willet	*Catoptrophorus semipalmatus*	MP	W, c
Wandering Tattler	*Heteroscelus incanus*	M	W, OS, L, c
Spotted Sandpiper	*Actitis macularia*	MP	W
Whimbrel	*Numenius phaeopus*	MP	W, c
Long-billed Curlew	*Numenius americanus*	M	W, c
Marbled Godwit	*Limosa fedoa*	MP	W, c
Ruddy Turnstone	*Arenaria interpres*	MP	W
Surfbird	*Aphriza virgata*	VM, C(2)	W, OS, L, c
Red Knot	*Calidris canutus*	MP	W, c
Sanderling	*Calidris alba*	MP	W, c
Semipalmated Sandpiper	*Calidris pusilla*	MP	W
Western Sandpiper	*Calidris mauri*	MP	W
Least Sandpiper	*Calidris minutilla*	M	W
Baird's Sandpiper	*Calidris bairdii*	T, C(1)	W, OS, L
Pectoral Sandpiper	*Calidris melanotos*	T	W
Stilt Sandpiper	*Calidris himantopus*	T	W
Buff-breasted Sandpiper	*Tryngites subruficollis*	T, C(1)	W
Short-billed Dowitcher	*Limnodromus griseus*	M	W
Long-billed Dowitcher	*Limnodromus scolopaceus*	VM, C(1), H	W, OS, L
Common Snipe	*Gallinago gallinago*	M	W, OS, L
Wilson's Phalarope	*Phalaropus tricolor*	T	W
Red-necked Phalarope	*Phalaropus lobatus*	M	W, c
Red Phalarope	*Phalaropus fulicaria*	T, H, C(2)	W, c
LARIDAE			
Pomarine Jaeger	*Stercorarius pomarinus*	T, H, C(2)	W, c
Parasitic Jaeger	*Stercorarius parasiticus*	VM, C(1), H	W, c
Long-tailed Jaeger	*Stercorarius longicaudus*	T, H, C(2)	W, c
Laughing Gull	*Larus atricilla*	M	W
Franklin's Gull	*Larus pipixcan*	T, M	W
Bonaparte's Gull	*Larus philadelphia*	VM, C(1), H	W, c
Ring-billed Gull	*Larus delawarensis*	M, H	W, c
California Gull	*Larus californicus*	VM, C(1)	W, c
Herring Gull	*Larus argentatus*	M	W, c
Sabine's Gull	*Xema sabini*	T, M	W, c
Gull-billed Tern	*Sterna nilotica*	MP	W, c
Caspian Tern	*Sterna caspia*	M	W
Royal Tern	*Sterna maxima*	MP	W, c
Elegant Tern	*Sterna elegans*	T	W, c
Sandwich Tern	*Sterna sandvicensis*	M	W, c
Roseate Tern	*Sterna dougallii*	T, C(1)	W
Common Tern	*Sterna hirundo*	M	W, c
Arctic Tern	*Sterna paradisaea*	T, C(1)	W, c
Forster's Tern	*Sterna forsteri*	VM, C(3)	W
Least Tern	*Sterna antillarum*	B, MP, D	W, c
Bridled Tern	*Sterna anaethetus*	VU, C(1), H	W, c
Sooty Tern	*Sterna fuscata*	T, C(1)	W, c
Black Tern	*Chlidonias niger*	M	W, c
Brown Noddy	*Anous stolidus*	T, C(1), H	W, c
RYNCHOPIDAE			
Black Skimmer	*Rynchops niger*	B, MP, d	W, OS, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
COLUMBIDAE			
Rock Dove	*Columba livia*	B	OG, AG
Red-billed Pigeon	*Columba flavirostris*	B	FG, AG
Band-tailed Pigeon	*Columba fasciata*	B, d	FG, H
White-winged Dove	*Zenaida asiatica*	B, MP	FG, OG, AG
Mourning Dove	*Zenaida macroura*	M	OG, L
Inca Dove	*Columbina inca*	B	OG, L
Common Ground-Dove	*Columbina passerina*	B	OS, L
Plain-breasted Ground-Dove	*Columbina minuta*	U	OS, L, w
Ruddy Ground-Dove	*Columbina talpacoti*	B	OG, L
Blue Ground-Dove	*Claravis pretiosa*	B, D	FS, L
Maroon-chested Ground-Dove	*Claravis mondetoura*	VU, EE, C(1)	FS, H, n
White-tipped Dove	*Leptotila verreauxi*	B	FG, L
White-faced Quail-Dove	*Geotrygon albifacies*	B, EE, D	FS, H, w
Ruddy Quail-Dove	*Geotrygon montana*	B, D	FS, L, w
PSITTACIDAE			
Green Parakeet	*Aratinga holochlora*	M, EE, D	FS, H
Pacific Parakeet	*Aratinga strenua*	B, d	FG, AG
Orange-fronted Parakeet	*Aratinga canicularis*	B, d	FG, L
Scarlet Macaw	*Ara macao*	U, X	FS, L, e
Orange-chinned Parakeet	*Brotogeris jugularis*	B, d	FG, L
White-fronted Parrot	*Amazona albifrons*	B, D	FS, L, w
Yellow-naped Parrot	*Amazona auropalliata*	B, D	FS, L
CUCULIDAE			
Black-billed Cuckoo	*Coccyzus erythropthalmus*	T, C(2)	OG, FG
Yellow-billed Cuckoo	*Coccyzus americanus*	T	FG, L
Mangrove Cuckoo	*Coccyzus minor*	B, MP?, d	FS, AG
Squirrel Cuckoo	*Piaya cayana*	B	FG, L
Striped Cuckoo	*Tapera naevia*	B	FG, L
Pheasant Cuckoo	*Dromococcyx phasianellus*	U, d	FS, L
Lesser Ground-Cuckoo	*Morococcyx erythropygus*	U	OS, L
Lesser Roadrunner	*Geococcyx velox*	B, EE, d	OG, H
Groove-billed Ani	*Crotophaga sulcirostris*	B	OG, AG
TYTONIDAE			
Barn Owl	*Tyto alba*	B, d	OG, L
STRIGIDAE			
Pacific Screech-Owl	*Otus cooperi*	B, d	FS, L
Whiskered Screech-Owl	*Otus trichopsis*	B, EE, d	FS, H, n
Crested Owl	*Lophostrix cristata*	VU, C(1)	FS, H
Spectacled Owl	*Pulsatrix perspicillata*	B, D	FS, L
Great Horned Owl	*Bubo virginianus*	U, D	FG, AG
Ferruginous Pygmy-Owl	*Glaucidium brasilianum*	B	FG, L
Burrowing Owl	*Athene cunicularia*	VM, C(3)	OS, L
Mottled Owl	*Ciccaba virgata*	B, d	FG, AG
Black-and-white Owl	*Ciccaba nigrolineata*	B, D	FS, L, w
Fulvous Owl	*Strix fulvescens*	U, E, D	FS, H, n
Striped Owl	*Pseudoscops clamator*	B, D	OS, L
Unspotted Saw-whet Owl	*Aegolius ridgwayi*	U, EE, D	FS, H, n
CAPRIMULGIDAE			
Lesser Nighthawk	*Chordeiles acutipennis*	B, MP, d	OS, L
Common Nighthawk	*Chordeiles minor*	VM, C(1), H	OG, AG
Pauraque	*Nyctidromus albicollis*	B	OG, L
Chuck-will's-widow	*Caprimulgus carolinensis*	T	FG, L
Whip-poor-will	*Caprimulgus vociferus*	B, MP, EE	FG, AG, H

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
NYCTIBIIDAE			
Northern Potoo	*Nyctibius jamaicensis*	U, D	OG, FG, L
APODIDAE			
Black Swift	*Cypseloides niger*	VU, C(3), H	OG, H
Chestnut-collared Swift	*Streptoprocne rutila*	U	OG, AG
White-collared Swift	*Streptoprocne zonaris*	U	OG, L
Chimney Swift	*Chaetura pelagica*	T, H, C(2)	OG, L
Vaux's Swift	*Chaetura vauxi*	U	OG, H
White-throated Swift	*Aeronautes saxatalis*	U	OG, H
Lesser Swallow-tailed Swift	*Panyptila cayennensis*	U, H	OG, L, w
Great Swallow-tailed Swift	*Panyptila sanctihieronymi*	U, H	OG, H, w
TROCHILIDAE			
Rufous Sabrewing	*Campylopterus rufus*	B, E, D	OS, H
Violet Sabrewing	*Campylopterus hemileucurus*	B	FG, H
Green Violet-ear	*Colibri thalassinus*	B, MP, d	OS, H
Green-breasted Mango	*Anthracothorax prevostii*	B, MP	OG, L
Emerald-chinned Hummingbird	*Abeillia abeillei*	U, E, D	FS, H, w
Canivet's Emerald	*Chlorostilbon canivetii*	B	FG, L
Blue-throated Goldentail	*Hylocharis eliciae*	B, D	FS, L
White-eared Hummingbird	*Hylocharis leucotis*	B, EE, d	FS, H, w
Azure-crowned Hummingbird	*Amazilia cyanocephala*	U, EE, d	FS, H, n
Berylline Hummingbird	*Amazilia beryllina*	U	FG, L
Blue-tailed Hummingbird	*Amazilia cyanura*	U	L, e
Cinnamon Hummingbird	*Amazilia rutila*	B	OG, L
Green-throated Mountain-gem	*Lampornis viridipallens*	U, E, EE(2), D	FS, H, w
Amethyst-throated Hummingbird	*Lampornis amethystinus*	U, EE, D	FS, H, n
Garnet-throated Hummingbird	*Lamprolaima rhami*	U, EE, D	FS, H, n
Magnificent Hummingbird	*Eugenes fulgens*	B, EE, d	OS, H
Long-billed Starthroat	*Heliomaster longirostris*	B, D	L
Plain-capped Starthroat	*Heliomaster constantii*	B, d	OG, L
Slender Sheartail	*Doricha enicura*	U, E, D	OS, H
Sparkling-tailed Hummingbird	*Tilmatura dupontii*	U, D	OS, H
Ruby-throated Hummingbird	*Archilochus colubris*	M	OG, FG, AG
Wine-throated Hummingbird	*Atthis ellioti*	U, E, EE, D	OS, H, w
TROGONIDAE			
Black-headed Trogon	*Trogon melanocephalus*	U, d	FS, L
Violaceous Trogon	*Trogon violaceus*	B, d	FG, L
Elegant Trogon	*Trogon elegans*	B, d	FG, L
Collared Trogon	*Trogon collaris*	B, D	FG, H, n
Resplendent Quetzal	*Pharomachrus mocinno*	B, EE, D	FS, H, n
MOMOTIDAE			
Tody Motmot	*Hylomanes momotula*	U, D	FS, L, w
Blue-throated Motmot	*Aspatha gularis*	B, E, D	FS, H, n
Blue-crowned Motmot	*Momotus momota*	B	FG, AG
Turquoise-browed Motmot	*Eumomota superciliosa*	B	OG, L
ALCEDINIDAE			
Ringed Kingfisher	*Ceryle torquata*	B, D	W, OS, L
Belted Kingfisher	*Ceryle alcyon*	M	W, OS, L
Amazon Kingfisher	*Chloroceryle amazona*	U, D	W, OS, L
Green Kingfisher	*Chloroceryle americana*	B, d	W, OS, L
American Pygmy Kingfisher	*Chloroceryle aenea*	B, d	FS, L, c
BUCCONIDAE			
White-necked Puffbird	*Notharchus macrorhynchos*	U, D	FS, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
RAMPHASTIDAE			
Emerald Toucanet	*Aulacorhynchus prasinus*	B, EE(2), D	FS, H
Collared Araçari	*Pteroglossus torquatus*	B, d	FG, L
PICIDAE			
Acorn Woodpecker	*Melanerpes formicivorus*	U, EE, d	FS, H, n
Golden-fronted Woodpecker	*Melanerpes aurifrons*	B	OG, FG, L
Yellow-bellied Sapsucker	*Sphyrapicus varius*	M	FG, H
Ladder-backed Woodpecker	*Picoides scalaris*	U	FG, AG, e
Hairy Woodpecker	*Picoides villosus*	U, EE, d	FS, H, n
Smoky-brown Woodpecker	*Veniliornis fumigatus*	B, D	FS, L
Golden-olive Woodpecker	*Piculus rubiginosus*	B	FG, AG
Northern Flicker	*Colaptes auratus*	B, EE, d	FS, H
Lineated Woodpecker	*Dryocopus lineatus*	B, d	FS, AG
Pale-billed Woodpecker	*Campephilus guatemalensis*	U, D	FS, L
FURNARIIDAE			
Rufous-breasted Spinetail	*Synallaxis erythrothorax*	B, d	OS, L
Scaly-throated Foliage-gleaner	*Anabacerthia variegaticeps*	U, D	FS, H, n
Ruddy Foliage-gleaner	*Automolus rubiginosus*	U, D	FS, H, n
DENDROCOLAPTIDAE			
Ruddy Woodcreeper	*Dendrocincla homochroa*	B, D	FS, L, w
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	U, d	FG, L
Strong-billed Woodcreeper	*Xiphocolaptes promeropirhynchus*	U, EE, D	FG, H
Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	B, D	FS, L
Ivory-billed Woodcreeper	*Xiphorhynchus flavigaster*	B, d	FG, L
Spotted Woodcreeper	*Xiphorhynchus erythropygius*	VU, EE?, C(2)	FS, H, n
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	B, d	FS, L
Spot-crowned Woodcreeper	*Lepidocolaptes affinis*	B, EE, d	FS, H
THAMNOPHILIDAE			
Barred Antshrike	*Thamnophilus doliatus*	B	OS, L
FORMICARIIDAE			
Scaled Antpitta	*Grallaria guatimalensis*	B, EE, D	FS, H, w
TYRANNIDAE			
Northern Beardless-Tyrannulet	*Camptostoma imberbe*	U, d	FS, L
Greenish Elaenia	*Myiopagis viridicata*	B	FG, L
Yellow-bellied Elaenia	*Elaenia flavogaster*	B	OG, L
Mountain Elaenia	*Elaenia frantzii*	B, EE, d	FG, OG, H
Ochre-bellied Flycatcher	*Mionectes oleagineus*	B, D	FS, L, w
Paltry Tyrannulet	*Zimmerius vilissimus*	B, d	FS, H, w
Northern Bentbill	*Oncostoma cinereigulare*	B, D	FS, L
Common Tody-Flycatcher	*Todirostrum cinereum*	B, d	OS, L
Eye-ringed Flatbill	*Rhynchocyclus brevirostris*	B, d	FS, H, w
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	B	FG, L
Stub-tailed Spadebill	*Platyrinchus cancrominus*	U, D	FS, L
Royal Flycatcher	*Onychorhynchus coronatus*	U, D	FS, L
Belted Flycatcher	*Xenotriccus callizonus*	U, E, D	FS, H
Tufted Flycatcher	*Mitrephanes phaeocercus*	U, EE, D	FS, H, n
Olive-sided Flycatcher	*Contopus cooperi*	T	FG, AG
Greater Pewee	*Contopus pertinax*	U, MP?, EE, d	FS, H, n
Western Wood-Pewee	*Contopus sordidulus*	T	FG, AG
Eastern Wood-Pewee	*Contopus virens*	T, H, C(2)	FG, L
Tropical Pewee	*Contopus cinereus*	B, MP?, d	FS, L
Yellow-bellied Flycatcher	*Empidonax flaviventris*	M	FG, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
Willow Flycatcher	*Empidonax traillii*	M	OG, L
White-throated Flycatcher	*Empidonax albigularis*	U, EE, D	OS, H
Least Flycatcher	*Empidonax minimus*	M	FG, L
Hammond's Flycatcher	*Empidonax hammondii*	M, d	FS, H, n
Yellowish Flycatcher	*Empidonax flavescens*	B, EE, d	FS, H
Buff-breasted Flycatcher	*Empidonax fulvifrons*	U, EE, d	FS, H, n
Black Phoebe	*Sayornis nigricans*	B, D	FS, L, w
Bright-rumped Attila	*Attila spadiceus*	B, D	FS, L
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	B	FG, AG
Ash-throated Flycatcher	*Myiarchus cinerascens*	VM, C(1)	L
Nutting's Flycatcher	*Myiarchus nuttingi*	U	OG, L
Great Crested Flycatcher	*Myiarchus crinitus*	M	FG, L
Brown-crested Flycatcher	*Myiarchus tyrannulus*	B, MP, d	FS, L
Great Kiskadee	*Pitangus sulphuratus*	B	OG, FG, L
Boat-billed Flycatcher	*Megarynchus pitangua*	B	FG, AG
Social Flycatcher	*Myiozetetes similis*	B	FG, L
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	BM	FG, L
Tropical Kingbird	*Tyrannus melancholicus*	B	OG, L
Western Kingbird	*Tyrannus verticalis*	M	OG, L
Eastern Kingbird	*Tyrannus tyrannus*	T	OG, AG
Scissor-tailed Flycatcher	*Tyrannus forficatus*	M	OG, L
INCERTAE SEDIS			
Gray-collared Becard	*Pachyramphus major*	U, EE, D	FS, H
Rose-throated Becard	*Pachyramphus aglaiae*	B	FG, L
Masked Tityra	*Tityra semifasciata*	B	FG, AG
PIPRIDAE			
Long-tailed Manakin	*Chiroxiphia linearis*	B, d	FS, L
VIREONIDAE			
Mangrove Vireo	*Vireo pallens*	U, D	FS, L, c
Bell's Vireo	*Vireo bellii*	M, d	OS, L
Yellow-throated Vireo	*Vireo flavifrons*	M, d	FG, L
Blue-headedVireo	*Vireo solitarius*	U, MP?, EE?, d	FS, H
Warbling Vireo	*Vireo gilvus*	M	FG, AG
Brown-capped Vireo	*Vireo leucophrys*	U, EE, D	FS, H, w
Philadephia Vireo	*Vireo philadelphicus*	M, d	FG, H
Red-eyed Vireo	*Vireo olivaceus*	T, C(2)	FG, AG
Yellow-green Vireo	*Vireo flavoviridis*	BM	FG, L
Lesser Greenlet	*Hylophilus decurtatus*	B	FG, L
Green Shrike-Vireo	*Vireolanius pulchellus*	U, D	FS, L, w
Rufous-browed Peppershrike	*Cyclarhis gujanensis*	B	FG, AG
CORVIDAE			
Steller's Jay	*Cyanocitta stelleri*	U, EE, D	FS, H, n
White-throated Magpie-Jay	*Calocitta formosa*	B	OG, AG
Brown Jay	*Cyanocorax morio*	VU, C(1)	FG, L, n
Bushy-crested Jay	*Cyanocorax melanocyaneus*	B, E, EE(2), d	FG, H
Black-throated Jay	*Cyanolyca pumilo*	B, E, D	FS, H, n
Unicolored Jay	*Aphelocoma unicolor*	U, EE, D	FS, H, n
Common Raven	*Corvus corax*	B, D	OG, H
HIRUNDINIDAE			
Gray-breasted Martin	*Progne chalybea*	B	OG, AG
Tree Swallow	*Tachycineta bicolor*	VM, C(2), H	OS, L
Mangrove Swallow	*Tachycineta albilinea*	B, d	W, FS, L
Violet-green Swallow	*Tachycineta thalassina*	M	OG, FG, AG

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
Black-capped Swallow	*Notiochelidon pileata*	B, E, d	OS, H, n
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	B, MP?	OG, AG?
Bank Swallow	*Riparia riparia*	T	OG, L
Barn Swallow	*Hirundo rustica*	M	OG, AG
Cliff Swallow	*Petrochelidon pyrrhonota*	T	OG, L
Cave Swallow	*Petrochelidon fulva*	M, d	OG, L
TROGLODYTIDAE			
Band-backed Wren	*Campylorhynchus zonatus*	B, d	OS, H, n
Rufous-naped Wren	*Campylorhynchus rufinucha*	B	OG, L
Rock Wren	*Salpinctes obsoletus*	B, EE, d	OS, H
Spot-breasted Wren	*Thryothorus maculipectus*	B, d	FS, OS, H
Rufous-and-white Wren	*Thryothorus rufalbus*	B, d	FS, AG
Banded Wren	*Thryothorus pleurostictus*	B, d	FS, L
Plain Wren	*Thryothorus modestus*	B	OG, AG
House Wren	*Troglodytes aedon*	B	OG, FG, H
Rufous-browed Wren	*Troglodytes rufociliatus*	B, E, EE(2), D	FS, H, w
Gray-breasted Wood-Wren	*Henicorhina leucophrys*	B, EE, D	FS, H, n
SYLVIIDAE			
Long-billed Gnatwren	*Ramphocaenus melanurus*	U, D	FS, L
Blue-gray Gnatcatcher	*Polioptila caerulea*	M, H	FG, L, n
White-lored Gnatcatcher	*Polioptila albiloris*	B, d	OS, L
TURDIDAE			
Eastern Bluebird	*Sialia sialis*	B, EE, d	FS, H
Brown-backed Solitaire	*Myadestes occidentalis*	B, EE, d	FS, H
Slate-colored Solitaire	*Myadestes unicolor*	U, D	FS, H, n
Orange-billed Nightingale-Thrush	*Catharus aurantiirostris*	B, d	FS, H
Ruddy-capped Nightingale-Thrush	*Catharus frantzii*	B, EE, D	FS, H, w
Spotted Nightingale-Thrush	*Catharus dryas*	U, EE, D	FS, H, n
Swainson's Thrush	*Catharus ustulatus*	M	FG, AG
Hermit Thrush	*Catharus guttatus*	VM, C(4)	FG, H
Wood Thrush	*Hylocichla mustelina*	M	FG, H
Black Robin	*Turdus infuscatus*	B, D	FS, H, w
Mountain Robin	*Turdus plebejus*	B, EE, D	FS, H, n
Clay-colored Robin	*Turdus grayi*	B, MP?	FG, AG
White-throated Robin	*Turdus assimilis*	B, EE, d	FS, H
Rufous-collared Robin	*Turdus rufitorques*	B, E, d	OS, H, w
Aztec Thrush	*Ridgwayia pinicola*	VM, C(1), H	FG, H
MIMIDAE			
Gray Catbird	*Dumetella carolinensis*	VM, C(3)	FG, H, w
Tropical Mockingbird	*Mimus gilvus*	B	OG, L
Blue-and-white Mockingbird	*Melanotis hypoleucus*	B, E, d	OS, H, w
MOTACILLIDAE			
American Pipit	*Anthus rubescens*	VM, C(2)	OS, AG
BOMBYCILLIDAE			
Cedar Waxwing	*Bombycilla cedrorum*	M	FG, AG
PEUCEDRAMIDAE			
Olive Warbler	*Peucedramus taeniatus*	U, EE, D	FS, H, n
PARULIDAE			
Blue-winged Warbler	*Vermivora pinus*	M	FG, H
Golden-winged Warbler	*Vermivora chrysoptera*	M, d	FG, H
Tennessee Warbler	*Vermivora peregrina*	M	FG, AG

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
Orange-crowned Warbler	*Vermivora celata*	VM, C(2), H	OG, H
Nashville Warbler	*Vermivora ruficapilla*	M	OG, H
Crescent-chested Warbler	*Parula superciliosa*	B, EE, d	FS, H
Northern Parula	*Parula americana*	T, C(1)	FG, L
Yellow Warbler	*Dendroica petechia*	B, MP, d	FS, L
Chestnut-sided Warbler	*Dendroica pensylvanica*	T, C(1)	
Magnolia Warbler	*Dendroica magnolia*	M	FG, L
Cape May Warbler	*Dendroica tigrina*	VM, C(2)	
Yellow-rumped Warbler	*Dendroica coronata*	M	OG, H
Golden-cheeked Warbler	*Dendroica chrysoparia*	VM, C(2), H, D	FG, H?, w
Black-throated Green Warbler	*Dendroica virens*	M	FG, AG
Townsend's Warbler	*Dendroica townsendi*	M	OG, FG, H
Hermit Warbler	*Dendroica occidentalis*	VM, C(4)	FS, H
Blackburnian Warbler	*Dendroica fusca*	T	FG, L
Yellow-throated Warbler	*Dendroica dominica*	VM, C(3)	FS, H
Grace's Warbler	*Dendroica graciae*	U, EE, d	FS, H, n
Prairie Warbler	*Dendroica discolor*	VM, C(2)	OG, FG, AG
Bay-breasted Warbler	*Dendroica castanea*	T, C(1)	FG
Black-and-white Warbler	*Mniotilta varia*	M	FG, AG
American Redstart	*Setophaga ruticilla*	M, d	FS, L
Prothonotary Warbler	*Protonotaria citrea*	M, d	FS, L
Worm-eating Warbler	*Helmitheros vermivorus*	M	FG, AG
Ovenbird	*Seiurus aurocapillus*	M	FG, AG
Northern Waterthrush	*Seiurus noveboracensis*	M, d	FS, L
Louisiana Waterthrush	*Seiurus motacilla*	M, d	FS, L
Kentucky Warbler	*Oporornis formosus*	T, M	FG, AG
Mourning Warbler	*Oporornis philadelphia*	T	OG, FG?, L
MacGillivray's Warbler	*Oporornis tolmiei*	M	OG, FG, H
Common Yellowthroat	*Geothlypis trichas*	M	OG, AG
Gray-crowned Yellowthroat	*Geothlypis poliocephala*	B, d	OS, AG
Hooded Warbler	*Wilsonia citrina*	M	FG, AG
Wilson's Warbler	*Wilsonia pusilla*	M	FG, H
Canada Warbler	*Wilsonia canadensis*	T	FG, AG
Red-faced Warbler	*Cardellina rubrifrons*	VM, C(3)	FG, H
Painted Redstart	*Myioborus pictus*	B, EE, d	FS, H, n
Slate-throated Redstart	*Myioborus miniatus*	B, EE, d	FS, H, w
Fan-tailed Warbler	*Euthlypis lachrymosa*	B, D	FS, L
Golden-crowned Warbler	*Basileuterus culicivorus*	U, D	FS, H, w
Rufous-capped Warbler	*Basileuterus rufifrons*	B	FG, AG
Golden-browed Warbler	*Basileuterus belli*	U, EE, D	FS, H, n
Yellow-breasted Chat	*Icteria virens*	M	OG, L
THRAUPIDAE			
Common Bush-Tanager	*Chlorospingus ophthalmicus*	U, EE, d	FS, H, n
Red-crowned Ant-Tanager	*Habia rubica*	B, D	FS, AG
Red-throated Ant-Tanager	*Habia fuscicauda*	B, d	FS, L
Hepatic Tanager	*Piranga flava*	U, EE, d	FS, H, n
Summer Tanager	*Piranga rubra*	M	FG, L
Western Tanager	*Piranga ludoviciana*	M	FG, AG
Flame-colored Tanager	*Piranga bidentata*	U, d	FS, H
White-winged Tanager	*Piranga leucoptera*	B, d	FS, H
Blue-gray Tanager	*Thraupis episcopus*	B	OG, L
Yellow-winged Tanager	*Thraupis abbas*	B	OG, AG
Scrub Euphonia	*Euphonia affinis*	B	FG, L
Yellow-throated Euphonia	*Euphonia hirundinacea*	B, d	FS, AG, w
Elegant Euphonia	*Euphonia elegantissima*	B, D	FG, H
Blue-crowned Chlorophonia	*Chlorophonia occipitalis*	B, D	FS, H, w
Red-legged Honeycreeper	*Cyanerpes cyaneus*	B, MP	FG, L

APPENDIX I. Continued.

Family English name	Scientific name	Status	Distribution
EMBERIZIDAE			
Blue-black Grassquit	*Volatinia jacarina*	B	OG, AG
White-collared Seedeater	*Sporophila torqueola*	B	OG, L
Ruddy-breasted Seedeater	*Sporophila minuta*	B	OS, L
Blue Seedcater	*Amaurospiza concolor*	VU, C(2)	w
Yellow-faced Grassquit	*Tiaris olivacea*	U	OG, H
Slaty Finch	*Haplospiza rustica*	VU, C(3)	FS, H, n
Cinnamon-bellied Flowerpiercer	*Diglossa baritula*	B, EE, D	OS, H, w
White-naped Brush-Finch	*Atlapetes albinucha*	B, EE(2), d	FS, H, w
Chestnut-capped Brush-Finch	*Buarremon brunneinuchus*	B, EE, D	FS, H, n
Prevost's Ground-Sparrow	*Melozone biarcuatum*	B, d	FS, H
White-eared Ground-Sparrow	*Melozone leucotis*	B, EE, D	FS, H, w
Stripe-headed Sparrow	*Aimophila ruficauda*	B	OG, L
Rusty Sparrow	*Aimophila rufescens*	B, EE(2), d	OS, H
Chipping Sparrow	*Spizella passerina*	B, MP, d	FS, H, n
Lark Sparrow	*Chondestes grammacus*	VM, C(3)	OS, L
Savannah Sparrow	*Passerculus sandwichensis*	VM, C(2), d	OS, L
Grasshopper Sparrow	*Ammodramus savannarum*	M, d	OS, AG
Lincoln's Sparrow	*Melospiza lincolnii*	M	OG, H
Rufous-collared Sparrow	*Zonotrichia capensis*	B, EE	OG, H
Dickcissel	*Spiza americana*	M	OG, L
CARDINALIDAE			
Grayish Saltator	*Saltator coerulescens*	B	OG, AG
Buff-throated Saltator	*Saltator maximus*	VU, C(1)	OS, AG
Black-headed Saltator	*Saltator atriceps*	B	OG, FG, AG
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	M	OG, FG, AG
Blue Bunting	*Cyanocompsa parellina*	B, d	FS, L
Blue Grosbeak	*Guiraca caerulea*	U, MP	OG, L
Indigo Bunting	*Passerina cyanea*	M, d	OS, L
Painted Bunting	*Passerina ciris*	M, d	OG, L
ICTERIDAE			
Red-winged Blackbird	*Agelaius phoeniceus*	B, d	OS, L
Eastern Meadowlark	*Sturnella magna*	U, d	OS, AG, w
Melodious Blackbird	*Dives dives*	B	OG, AG
Great-tailed Grackle	*Quiscalus mexicanus*	B	OG, AG
Bronzed Cowbird	*Molothrus aeneus*	B	OG, AG
Black-vented Oriole	*Icterus wagleri*	U, d	FS, H, n
Bar-winged Oriole	*Icterus maculialatus*	B, E, D	FS, H
Orchard Oriole	*Icterus spurius*	M	OG, L
Yellow-backed Oriole	*Icterus chrysater*	U, d	FS, H, n
Streak-backed Oriole	*Icterus pustulatus*	B	OG, FG, AG
Spot-breasted Oriole	*Icterus pectoralis*	B, d	OG, FG, L
Altamira Oriole	*Icterus gularis*	B	OG, FG, L
Baltimore Oriole	*Icterus galbula*	M	OG, FG, L
Bullock's Oriole	*Icterus bullockii*	VM, C(2)	OG, AG
Yellow-billed Cacique	*Amblycercus holosericeus*	B	FG, L
Yellow-winged Cacique	*Cacicus melanicterus*	VU, C(1), H	OG, FG, L
FRINGILLIDAE			
Red Crossbill	*Loxia curvirostra*	VU, EE, C(1), H	FS, H, n
Black-headed Siskin	*Carduelis notata*	B, EE, d	FS, H, n
Lesser Goldfinch	*Carduelis psaltria*	B	OG, AG
Hooded Grosbeak	*Coccothraustes albeillei*	B, EE, D	FS, H, n
PASSERIDAE			
House Sparrow	*Passer domesticus*	B	OG, L

[a] KEY TO STATUS CODES: B = Breeding confirmed: BM = Breeding visitor; C = Casual (number of reports given in parentheses); d = Threatened; D = In danger of extirpation; E = Endemic to northern Central America; EE = Subspecies endemic to northern Central America (number indicates how many endemic subspecies occur in El Salvador if more than one); H = Hypothetical; M = Migratory winter visitor; MP = Partially migratory; T = Transient; U = Status uncertain (suspected to breed); VM = Migratory vagrant (visitor or transient status uncertain); VU = Non-migratory vagrant—breeding status uncertain; KEY TO DISTRIBUTION CODES: AG = Altitudinal generalist; FG = Forest generalist; FS = Forest specialist; H = Mainly in highlands; L = Mainly in lowlands; OG = Open habitat generalist; OS = Open habitat specialist; W = Water habitat specialist (c = coastal; c = east; n = north; w = west).

APPENDIX II. List of bird species expected to occur in El Salvador but not reported.

Family	English name	Scientific name
PROCELLARIIDAE	Kermadec Petrel	*Pterodroma neglecta*
	Juan Fernandez Petrel	*Pterodroma externa*
	Dark-rumped Petrel	*Pterodroma phaeopygia*
	Tahiti Petrel	*Pterodroma rostrata*
	Parkinson's Petrel	*Procellaria parkinsoni*
	Pink-footed Shearwater	*Puffinus creatopus*
	Sooty Shearwater	*Puffinus griseus*
	Christmas Shearwater	*Puffinus nativitatis*
	Townsend's Shearwater	*Puffinus auricularis*
HYDROBATIDAE	Leach's Storm-Petrel	*Oceanodroma leucorhoa*
	Wedge-rumped Storm-Petrel	*Oceanodroma tethys*
	Least Storm-Petrel	*Oceanodroma microsoma*
ANATIDAE	Wood Duck	*Aix sponsa*
	Cinnamon Teal	*Anas cyanoptera*
	Canvasback	*Aythya valisineria*
	Redhead	*Aythya americana*
	Ring-necked Duck	*Aythya collaris*
ACCIPITRIDAE	Black-and-white Hawk-Eagle	*Spizastur melanoleucus*
FALCONIDAE	Red-throated Caracara	*Daptrius americanus*
CRACIDAE	Plain Chachalaca	*Ortalis vetula*
ODONTOPHORIDAE	Spotted Wood-Quail	*Odontophorus guttatus*
RALLIDAE	Virginia Rail	*Rallus limicola*
HELIORNITHIDAE	Sungrebe	*Heliornis fulica*
SCOLOPACIDAE	Upland Sandpiper	*Bartramia longicauda*
	Hudsonian Godwit	*Limosa haemastica*
LARIDAE	South Polar Skua	*Catharacta maccormicki*
	Heermann's Gull	*Larus heermanni*
PSITTACIDAE	Barred Parakeet	*Bolborhynchus lineola*
STRIGIDAE	Flammulated Owl	*Otus flammeolus*
	Bearded Screech-Owl	*Otus barbarus*
	Vermiculated Screech-Owl	*Otus guatemalae*
	Northern Pygmy-Owl	*Glaucidium gnoma*
	Central American Pygmy-Owl	*Glaucidium griseiceps*
	Stygian Owl	*Asio stygius*
CAPRIMULGIDAE	Buff-collared Nightjar	*Caprimulgus ridgwayi*
APODIDAE	White-chinned Swift	*Cypseloides cryptus*
TROCHILIDAE	White-necked Jacobin	*Florisuga mellivora*
	Black-crested Coquette	*Lophornis helenae*
	White-bellied Emerald	*Amazilia candida*
	Stripe-tailed Hummingbird	*Eupherusa eximia*
	Broad-tailed Hummingbird	*Selasphorus platycercus*
TROGONIDAE	Mountain Trogon	*Trogon mexicanus*
PICIDAE	Hoffmann's Woodpecker	*Melanerpes hoffmanni*
FURNARIIDAE	Tawny-throated Leaftosser	*Sclerurus mexicanus*
DENDROCOLAPTIDAE	Black-banded Woodcreeper	*Dendrocolaptes picumnus*
TYRANNIDAE	Pine Flycatcher	*Empidonax affinis*
	Cassin's Kingbird	*Tyrannus vociferans*
	Thick-billed Kingbird	*Tyrannus crassirostris*

APPENDIX II. Continued.

Family	English name	Scientific name
VIREONIDAE	Hutton's Vireo	*Vireo huttoni*
	Chestnut-sided Shrike-Vireo	*Vireolanius melitophrys*
CORVIDAE	Green Jay	*Cyanocorax yncas*
	Azure-hooded Jay	*Cyanolyca cucullata*
HIRUNDINIDAE	Purple Martin	*Progne subis*
	Blue-and-white Swallow	*Notiochelidon cyanoleuca*
AEGITHALIDAE	Bushtit	*Psaltriparus minimus*
CERTHIIDAE	Brown Creeper	*Certhia americana*
TROGLODYTIDAE	Sedge Wren	*Cistothorus platensis*
	White-breasted Wood-Wren	*Henicorhina leucosticta*
CINCLIDAE	American Dipper	*Cinclus mexicanus*
REGULIDAE	Golden-crowned Kinglet	*Regulus satrapa*
	Ruby-crowned Kinglet	*Regulus calendula*
TURDIDAE	Black-headed Nightingale-Thrush	*Catharus mexicanus*
	Gray-cheeked Thrush	*Catharus minimus*
PTILOGONATIDAE	Gray Silky-flycatcher	*Ptilogonys cinereus*
PARULIDAE	Tropical Parula	*Parula pitiayumi*
	Pink-headed Warbler	*Ergaticus versicolor*
COEREBIDAE	Bananaquit	*Coereba flaveola*
EMBERIZIDAE	Spotted Towhee	*Pipilo maculatus*
	Botteri's Sparrow	*Aimophila botterii*
	Yellow-eyed Junco	*Junco phaonotus*
ICTERIDAE	Montezuma Oropendola	*Psarocolius montezuma*
FRINGILLIDAE	Pine Siskin	*Carduelis pinus*
	Black-capped Siskin	*Carduelis atriceps*

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DISTRIBUTION AND CONSERVATION OF BIRDS OF NORTHERN CENTRAL AMERICA

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ABSTRACT.—Patterns of distribution, diversity, and endemism in the birds of northern Central America were analyzed based on 541 avian species in 24 biotic regions. Many contrasts were apparent. For example, whereas species richness was concentrated in the Atlantic lowlands, with the Pacific lowlands, interior valleys, montane areas, and the Yucatan Peninsula less diverse; species endemic to the entire region were concentrated in the mountains and in the Yucatan Peninsula. Geographic patterns of endemism presented contrasts depending on the spatial scale of analysis. In contrast to overall patterns, species narrowly endemic to single geographic units were concentrated along the Pacific Coast of Chiapas and in southern Veracruz. Conservation implications of these results were explored using complementarity algorithms, producing ordered regional priority lists for the creation of optimal reserve systems. Finally, a plan of action for the study and conservation of avian diversity in northern Central America is outlined, including elements of basic inventory, systematics, and geographic analysis.

Some of the earliest studies of New World tropical birds were in Central America, including the impressive summary produced by Salvin and Godman (1879–1904). These early studies, in combination with subsequent investigations, led to treatments for each country and region: Chiapas (Álvarez del Toro 1971), southern Veracruz (Lowery and Dahlquest 1951), the Yucatan Peninsula (Paynter 1955), Guatemala (Griscom 1932, Land 1970), Belize (Russell 1964), Honduras (Monroe 1968), El Salvador (Dickey and van Rossem 1930, Thurber et al. 1987), and Nicaragua (Howell, unpubl. ms.). Hence, at first glance the region seems well known ornithologically, and not in need of intensive study.

Ornithological research has been sporadic and superficial, with no comprehensive survey of the entire region. Although wars and political conflicts that have characterized the last thirty years have largely ended, ornithological attention (apart from the other contributions to this symposium) has been slow to focus on the region. Hence, our purpose in this paper is to synthesize a distributional overview of the birds of northern Central America, which, although based on imprecise and incomplete information, is intended to detect general patterns in the region's avifauna. Our hope is that this preliminary summary will stimulate renewed attention to the region, especially by workers employing new techniques such as molecular genetics, phylogenetic systematics, and geographic information systems. We also make suggestions regarding the direction and context of new efforts of study and conserve the birds of northern Central America.

METHODS

For the purposes of this study, we defined northern Central America as extending from the Isthmus of Tehuantepec and southern Veracruz south and east through the Yucatan Peninsula, Chiapas, Guatemala, Belize, El Salvador, and Honduras, to western Nicaragua. This region forms a biogeographic unit (Dinerstein et al. 1995) clearly related to the historical sea channels that eventually closed to form the Central American isthmus (Stehli and Webb 1985, Mann 1995). We divided the region into 24 geographic regions that were homogeneous in terms of habitat makeup and biotic continuity (Fig. 1). For a few regions, such as the pine savannas and rain forests of the Mosquitia region of northern Honduras and Nicaragua, potentially distinct regions and habitat types were lumped because we lacked precise data.

We created a data base summarizing distributions of 541 bird species in the regions. Because our intent was to focus on distributional patterns of terrestrial bird species, only resident, breeding land bird species were included. Sources included the regional treatments cited above, surveys of museum specimens (for Mexico principally, see Acknowledgments), Hernández-Baños and coworkers (1995) and Howell and Webb (1995). We scored species as present or absent in each region; species' distributions beyond the limits of the study area were indicated as extending farther north or far-

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FIG 1. Map showing the 24 biotic regions employed in this study, with abbreviations used for reference in other figures.

ther south, based on the taxonomy and range descriptions in AOU (1983).

Subsequent analyses included UPGMA clustering of simple matching coefficient distances among regions derived from presence-absence matrices (Rohlf 1988). Near-optimal reserve combinations were obtained by means of a complementarity algorithm, implemented as follows: (1) series of criteria (e.g., species richness, endemism) were chosen and set in a specific order of importance; (2) a reserve was chosen based on the first criterion; (3) a second reserve was added based on the cumulative total for the first criterion (i.e., based on new species added to the total); (4) additional reserves were added one by onc based on their effect on the cumulative species total. In case of a tie, the second criterion was used to decide among tied possibilities; further criteria were used in the event of ties in the second criterion. Because of the large numbers of species involved, globally optimal approaches (e.g., Church et al. 1996) were impractical to implement (Pressey et al. 1996).

RESULTS

Overall bird species richness was unevenly and nonrandomly distributed in northern Central America (Fig. 2A). Highest numbers of species were found in the Atlantic lowlands from southern Mexico south to Nicaragua, and species richness was lower on the Yucatan Peninsula and in the interior and Pacific portions of the region. Lowest species richness was found in the interior valleys, probably reflecting isolation or paucity of microhabitats in their arid habitats, as well as in the mountains and Pacific lowlands of Nicaragua.

Cluster analyses of the overall data set revealed five principal groupings of areas (Fig. 3): (1) the Atlantic lowlands exclusive of the Yucatan Peninsula, (2) Pacific lowlands, (3) interior valleys, (4) the Yucatan Peninsula, and (5) montane areas. The montane areas were most distinct from the remaining four clusters. Within the latter grouping, the Atlantic lowlands were most distinctive, followed by the Yucatan Peninsula; the Pacific lowlands, and interior valleys grouped closely together. The only geographically disparate areas that grouped together were the Yucatan Peninsula, the Pacific lowlands and interior valleys, reflecting their common semiarid tropical faunal elements. Hence, patterns of faunal similarity among regions appear to correspond to geographic proximity and/or habitat similarity.

FIG. 2. Maps showing the geographic distribution of diversity of birds in northern Central America. Shown are (A) total numbers of species, (B) species endemic to northern Central America, (C) species restricted to five or fewer regions, and (D) species restricted to a single region.

Of the 541 species included in the data set, 150 (27.7%) ranged farther south than the study area, 138 (25.5%) ranged farther north, and 208 (38.4%) ranged both to the south and to the north. The remaining 45 (8.3%) occurred nowhere but in northern Central America (Table 1). The geographic distribution of these endemic species was highly localized (Fig. 2B): montane regions were major foci, and the Yucatan Peninsula contained a secondary concentration. Hence, patterns of endemism contrasted sharply with patterns of species richness.

Five avian genera were endemic to the region. The guans *Penelopina* and *Oreophasis* are both restricted to montane portions of the region. The motmot *Aspatha* is widely distributed; the turkey *Agriocharis* occurs throughout the Petén region (although submerged in *Meleagris* by AOU 1995); and the mimid *Melanoptila* is found only on the Yucatan Peninsula. Because all five are monotypic genera, no secondary speciation within the region appears to have taken place.

Clustering regions based on the distribution of endemic species revealed patterns similar to those recovered from analysis of all species (Fig. 3). Again, montane regions were most

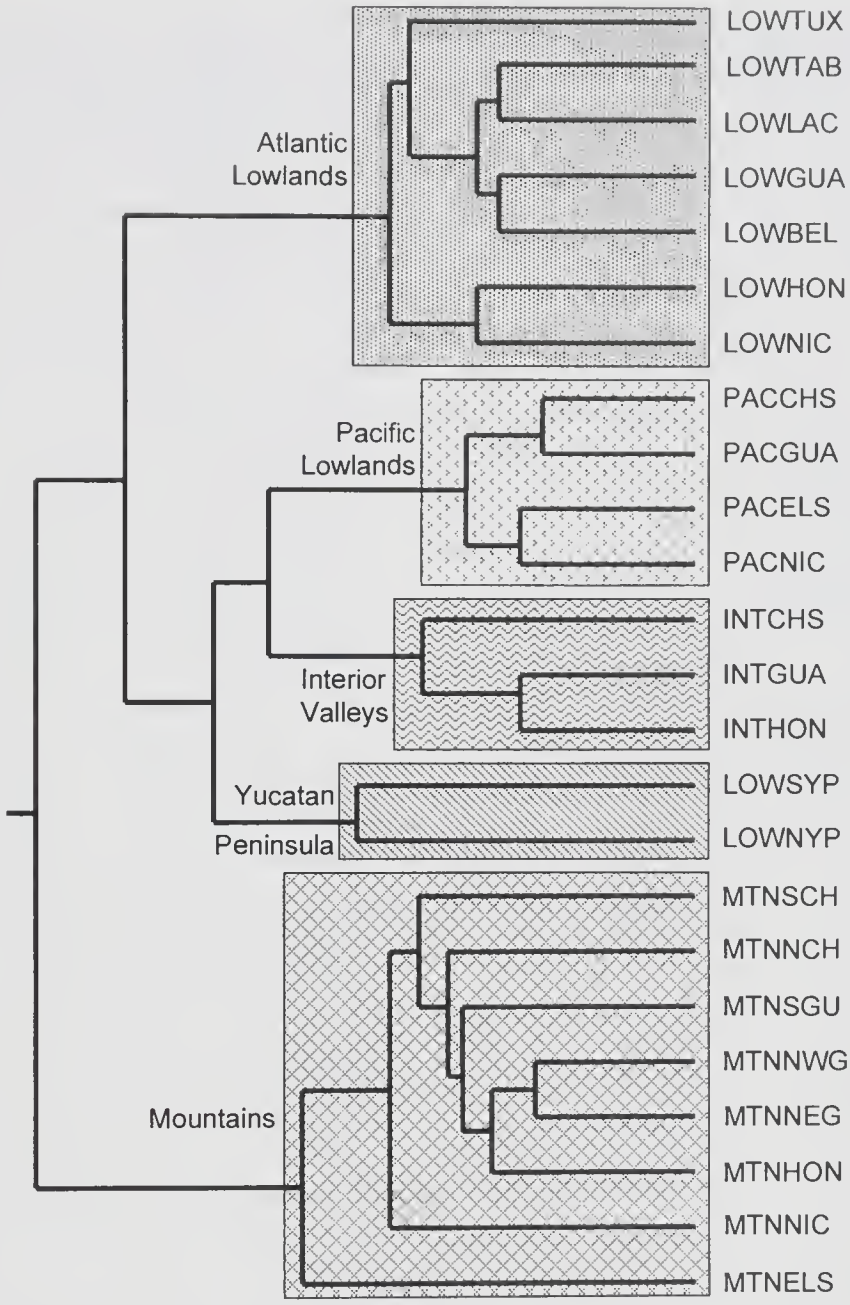

FIG. 3. Cluster analysis showing patterns of avifaunal similarity among regions based on all species. Abbreviations for regions given in Fig. 1.

distinctive, and clusters were recognizable for the Yucatan Peninsula and other lowland areas, although patterns were not as well defined as for the overall analysis. Hence, the fewer species involved in the endemic cluster analysis probably led to less clear overall resolution.

Examination of the spatial scale of endemism showed that endemic species' ranges included as few as one region (8 spp.), up to a maximum of 10 regions (1 spp.; Table 1). Regional endemics were concentrated in montane areas and in the Yucatan Peninsula (Fig. 2B). When only species found in five regions or fewer were considered, the Yucatan Peninsula had a higher concentration (Fig. 2C). The eight species restricted to single regions ("narrow endemics"), were found in the Pacific lowlands of Chiapas (*Passerina rositae, Aimophila sumichrasti, Campylorhynchus chiapensis*), the Los Tuxtlas region of southern Veracruz (*Campylopterus excellens, Geotrygon carrikeri*) and include 3 species in 3 other regions (Fig. 2D). Hence, foci of endemism vary strikingly depending on the spatial scale of the analysis.

TABLE 1. List of bird species endemic to northern Central America, with number of regions in which the species occurs.

Species	Number of regions
Agriocharis ocellata	5
Aimophila sumichrasti	1
Amazilia luciae	1
Amazona xantholora	2
Aratinga strenua	6
Arremonops chloronotus	6
Aspatha gularis	6
Atthis ellioti	7
Campylopterus excellens	1
Campylopterus rufus	5
Campylorhynchus chiapensis	1
Campylorhynchus yucatanicus	1
Caprimulgus badius	2
Carduelis atriceps	4
Colinus nigrogularis	4
Cyanocorax melanocyaneus	10
Cyanocorax yucatanicus	6
Cyanolyca pumilo	6
Cyrtonyx ocellatus	7
Doricha enicura	7
Ergaticus versicolor	5
Geotrygon carrikeri	1
Granatellus sallaei	6
Icterus auratus	2
Icterus maculialatus	4
Lampornis sybillae	2
Lampornis viridipallens	7
Melanerpes hoffmannii	1
Melanerpes pygmaeus	2
Melanoptila glabrirostris	4
Melanotis hypoleucus	7
Myiarchus yucatanensis	4
Notiochelidon pileata	7
Nyctiphrynus yucatanicus	3
Oreophasis derbianus	5
Ortalis leucogastra	4
Otus barbarus	3
Passerina rositae	1
Penelopina nigra	7
Piranga roseogularis	3
Strix fulvescens	7
Tangara cabanisi	2
Troglodytes rufociliatus	8
Turdus rufitorques	7
Xenotriccus callizonus	3

DISCUSSION

Conservation priorities.—The analyses presented above, although preliminary, have interesting implications for the conservation of avian diversity in northern Central America. Most importantly, overall patterns of avian species richness and endemism contrasted sharply, leading to a quandary for conservation prioritization: species richness was highest in the Atlantic lowlands, whereas endemism was greatest in montane regions and in the Yucatan Peninsula (Fig. 2A, B). Similar results have been encountered elsewhere and at other scales of analysis, making the generality of the result convincing (Escalante-Pliego et al. 1993, Peterson et al. 1993, Hernández-Baños et al. 1995, Peterson and Salazar, in press).

To add further complication, "endemism" can be defined in several ways. Although the simplest version is "found nowhere else," a case can be made for the importance of considering range size as well to identify endemic species (ICBP 1992). Unfortunately, geographic concentrations of endemism may differ based on spatial scale and definition used (Figure 2B–D), making identification of priorities complex.

Another complication for implementation of conservation policies is the lack of information on available habitat. The spatial extent and geographic distribution of patches of primary habitat remaining in northern Central America remain unassessed. Without this critical information, design of adequate strategies for conservation at a fine scale is all but impossible. Hence, evaluation of geographic patterns of land use and habitat distribution would represent an important advance in biodiversity conservation in the region.

A variety of approaches can be used to establish priorities for creating references. If geographic patterns in species richness and endemism were coincident, an optimal strategy would be to represent each of the principal assemblages in the cluster analysis in a reserve system (Peterson and Salazar, in press). Because such coincidence is lacking in the present case, we have taken a more quantitative approach based on the principle of complementarity among reserves in the system.

Under the assumption that a reserve within a particular region should hold the important components of the region's biodiversity, we performed two complementarity analyses based on different criteria. The first maximized representation of single-region endemics. In cases where this criterion was equivo-

cal, we used representation of endemic species with ranges of five or fewer regions; succeeding criteria were overall endemism and species richness (Fig. 4). Under this approach, the optimal reserve system included (in order of decreasing importance) the following areas: Pacific lowlands of Chiapas, Los Tuxtlas, northern Yucatan Peninsula, Atlantic lowlands of Honduras, Pacific lowlands of Nicaragua, Sierra Norte of Chiapas, interior valley of Chiapas, mountains of Nicaragua, southern Yucatan Peninsula, and mountains of southern Guatemala. This prioritization therefore represents a near-optimal combination of reserves in regions of Central America for the preservation of avian diversity, emphasizing restricted-range endemics.

An alternative approach emphasized species richness, followed by overall endemism, five-region endemics, and single-region endemics (Fig. 4). Under this prioritization, first in importance were the Atlantic lowlands of Honduras, followed by the Sierra Norte of Chiapas, southern Yucatan Peninsula, Pacific lowlands of Chiapas, interior valley of Chiapas, mountains of southern Guatemala, Los Tuxtlas, northern Yucatan Peninsula, mountains of Nicaragua, and Tabasco. This list therefore represents a near-optimal reserve scheme for preserving bird diversity by emphasizing species richness.

The two complementarity implementations yielded highly noncoincident results, suggesting that hard decisions may be required for conservation efforts to proceed. Comparing rankings for areas included in both systems yielded an r^2 of 0.001 (Spearman rank correlation), indicating little or no association. Hence, conservation efforts must begin by choosing an order of importance for the different dimensions of biodiversity to make prioritization of different areas possible. We suggest that the restricted-range endemics are at much greater risk of extinction and that their prioritization should be accorded precedence.

Spatial scale of endemism.—An additional consideration for the use of endemism in conservation planning springs from the examination of distribution of endemism at different spatial scales, pointing out the danger of areal definitions of endemism in biodiversity studies. Fig. 2 illustrates the changing nature of foci of endemism based on different spatial definitions; whereas regional endemism is focused in montane regions and the Yucatan Peninsula, narrow endemics are concentrated along the Pacific lowlands of Chiapas and in Los Tuxtlas. Similar results have been obtained in studies of other avian assemblages (Hernández-Baños et al. 1995), suggesting that endemism defined at different spatial scales may not always yield coincident results.

A worrisome implication of this result regards recent studies of avian endemism on a worldwide scale. ICBP (1992) defined species with total ranges of 50,000 km^2 or less as endemics, and analyzed their geographic distribution to establish priority zones for conservation attention. These results suggest that such studies may yield pictures of endemism that are highly unstable and unpredictable depending on their position along some unknown spectrum as seen in Fig. 2. Hence, the conclusions reached by ICBP (1992) and other studies imposing single spatial definitions on endemism may prove to reflect only one dimension of endemism, rather than some single underlying pattern.

Future directions.—Based on the analyses presented above and on our understanding of present ornithological activity in northern Central America, we suggest three general research areas that need much more activity. These topics are inventory, systematics, and geographic analysis—thorough, synthetic studies in each realm would greatly improve the knowledge and understanding of the region's avifauna.

A first, and most critical, need is for basic avifaunal inventories. These studies document details of distribution for each species, and permit understanding community composition, inferring historical geographic patterns, determining conservation priorities, and many other important facets of the geography and ecology of bird species. Properly documented by voucher specimens (Remsen 1995), and other associated data, inventories can serve as the foundation for many systematic and geographic studies as well.

An example of the dire need for basic inventory studies can be taken from a two-week study in 1993 on Cerro Piedra Larga, Oaxaca, Mexico (Escalona-Segura et al., unpubl. data). This mountain, although in close proximity to well-known sites in a thoroughly documented

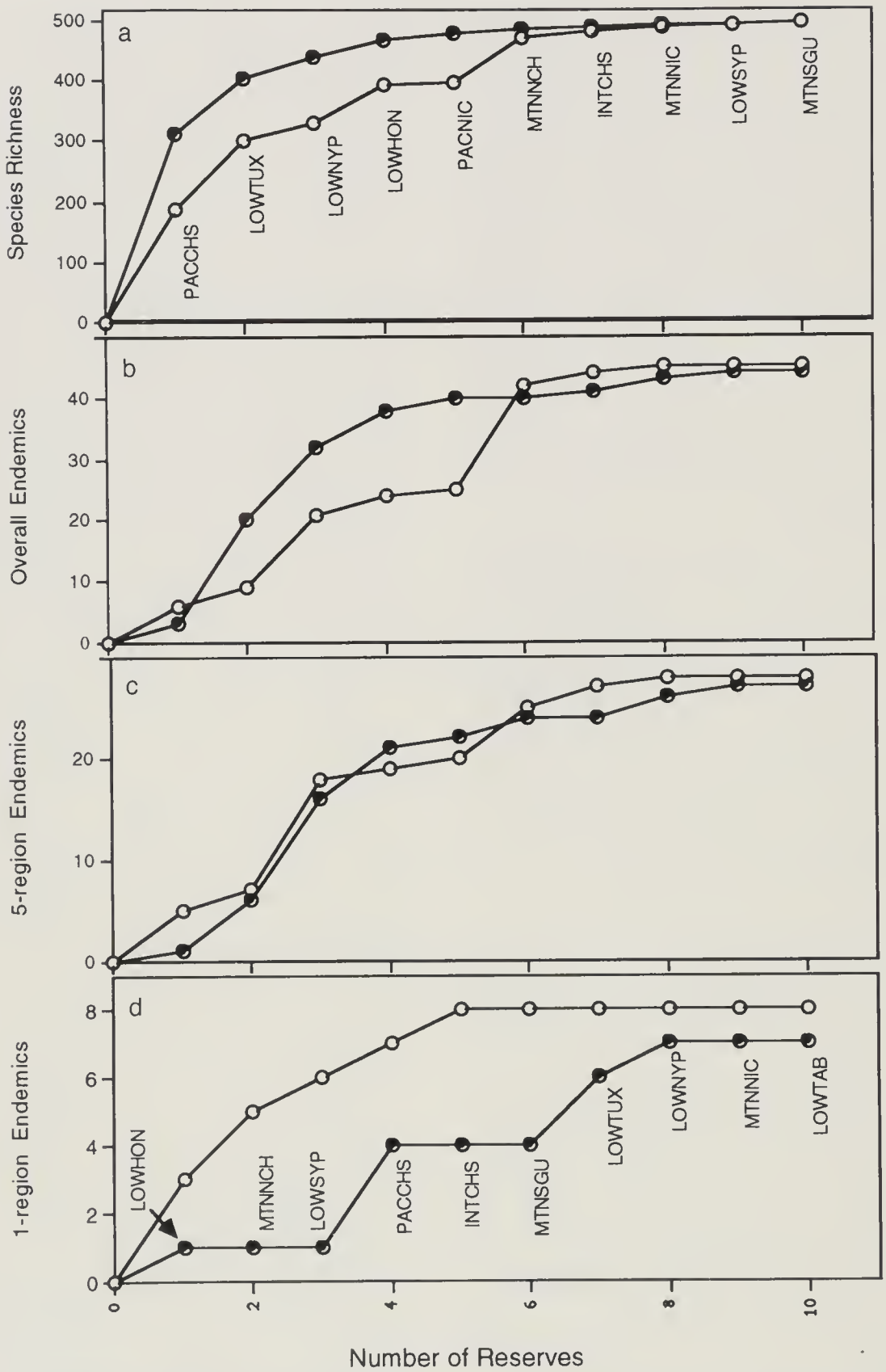

FIG. 4. Cumulative graphs of representation of species in reserve systems in northern Central America, based on criteria ranked as species richness, overall endemism, endemics to 5 or fewer regions, and endemics to single regions (closed symbols), and based on criteria ranked as endemics to single regions, endemics to five or fewer regions, overall endemism, and species richness (open symbols). A. Total species richness, B. Overall endemics, C. Endemics restricted to five regions, D. Endemics restricted to one region. Abbreviations for regions are from Fig. 1.

state (Binford 1989), is isolated between the southeastern termini of the Sierra de Miahuatlán and the Sierra de los Mixes. It had never been surveyed ornithologically—the expectation was that its fauna would be allied with that of one mountain range or the other (Hernández-Baños et al. 1995). After careful study, however, we found three forms of eastern affinity (Sierra de los Mixes), mixed with four of western affinity (Sierra de Miahuatlán), making the mountain a fascinating and unique mix of the distinct avifaunas of the neighboring mountain ranges. Other unexpected discoveries, such as the rare Maroon-fronted Ground-Dove (*Claravis mondetoura*) and the first-known sympatry of two differentiated populations of the Amethyst-throated Hummingbird (*Lampornis amethystinus*), further serve to illustrate the importance of these basic studies. Many other sites throughout northern Central America remain unsurveyed or inadequately sampled; hence, much remains to be learned about the birds of the region.

Systematic studies form an important second element in our proposed plan of action. Although the taxonomy, distribution, ecology, and variation of birds appear to be generally well documented (e.g., AOU 1983), in fact, much remains to be studied. Major methodological and theoretical advances in systematics in the past three decades have been applied to only a few species in Mesoamerica. As a result, most species' taxonomy has seen no recent systematic attention, making modern study imperative.

Much systematic work will prove necessary to delineate the species-level taxa of birds in northern Central America. With respect to Mexican birds, ongoing systematic studies have identified many species-level units that need to be recognized for a full appreciation of the dimensions of avian biodiversity—for example, multiple species are recognizable within all three currently recognized *Aphelocoma* jays (Peterson 1992), Acorn Woodpeckers (*Melanerpes formicivorus*; Benítez-Díaz 1992), *Cypseloides* swifts (Navarro-Sigüenza et al. 1992), *Geotrygon* quail-doves (Peterson 1993), Rosy-throated Thrush-Tanager (*Rhodinocichla rosea*; Peterson et al., unpubl. data), House Wren (*Troglodytes aedon*; Escalona-Segura 1995), and many others. More than 50 complexes remain in need of study, including newly recognized forms that would increase the number of species endemic to Mexico by at least 240% (Navarro-Sigüenza and Peterson, unpubl. data)! Although action in creation of reserves should not await these detailed examinations, these changes will influence the picture of biodiversity in Mexico and other northern Central American countries.

Thirdly, explorations of the application of synthetic geographic approaches to biodiversity questions in northern Central America are badly needed. The results presented above are the crudest of beginnings, based on imprecise data and a subjective regionalization. More sophisticated approaches would permit many improvements. For example, known occurrence points for species can be associated with thematic geographic factors to produce statistical models of the probability of species' occurrence across the landscape (e.g., Miller et al. 1989, Walker and Cocks 1991, Hollander et al. 1994). Remote sensing approaches can be used to characterize the distribution and limits of large extents of primary habitat (Skole and Tucker 1993). Finally, synthetic approaches can overlay predicted species' ranges to form "biodiversity maps," which can be compared with geographic features using landscape metrics (Van Dorp and Opdam 1987, Hejl 1992) and used to situate conservation areas (Harrison and Martinez 1995). Synthetic analyses will prove instructive and informative about many previously unappreciated details of biodiversity, especially in exceptionally diverse and little-studied tropical regions like northern Central America.

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ORNITHOLOGY IN BELIZE SINCE 1960

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ABSTRACT.—We review ornithology in Belize, formerly British Honduras, since Russell's 1964 monograph and summarize published and unpublished reports, banding records, and museum data. Unpublished reports (gray literature) are an important source of information within the country. Since 1960, there have been numerous studies by the British Forces ornithological societies and others on avian ecology and behavior, the effects of logging on birds, the distribution of overwintering Neotropical migrants (approximately 20% of Belize's avifauna), and comparisons of avian distribution in disturbed versus undisturbed habitat. We review recent distributional records and problematic species records requiring verification and identify distributional "knowledge gaps". Although 70% of the country is still dominated by natural vegetation and 20% falls under some form of protected status, certain bird species and families are at risk from human impacts such as habitat conversion, hunting, introduced species, and in some cases, tourism. Areas for future study are suggested.

Russell (1964) provided a synopsis of ornithology in Belize through the early 1960s in his monograph: A Distributional Study of the Birds of British Honduras. In this comprehensive work he reviewed historical ornithological work in the country as far back as the 1800s. Our purpose here is not to reiterate Russell's exhaustive work, but to offer an update on ornithological study in Belize. We have divided such studies into broad categories that include ecological and behavioral studies and distributional updates. Although not strictly distributional in nature, we discuss banding records that add to our knowledge of avian distribution.

METHODS

Sources of Information.—In this paper we draw on information from many sources, including both published and unpublished literature. Unpublished reports, or "gray literature," are sometimes the only sources of information available to researchers in developing countries because scientific journals are generally costly and postal services may be unreliable. Although not critically reviewed, such unpublished resources frequently offer valuable, localized information not available otherwise. Such reports are often heavily used by government officials and decision makers. A source of such literature is BIODOC, Centro de Documentacion en Vida Silvestre, a cooperative effort between the Universidad Nacional, Costa Rica and the U.S. Fish and Wildlife Service. Research permits issued in Belize stipulate that a copy of any report resulting from such research be provided to the Forest Department, Ministry of Natural Resources. Within the active NGO community, there are three repositories for natural history information: the Belize Audubon Society being the longest standing and possibly most complete, the Belize Zoo and Tropical Education Center, and the Programme for Belize.

In the future, such reports should become more accessible to those outside the country as well as those within. The Conservation and Environmental Data System (CEDS) under the auspices of the Land Information Centre, Ministry of Natural Resources, intends to make such resources more widely available. CEDS has, as its primary mission, the development of a master catalog of such literature. Cataloging is well underway, and includes both government and NGO holdings relevant to conservation and environmental concerns within Belize. The CEDS literature resource database will be accessible via a telephone modem link allowing members to search what might be thought of as a national de-centralized library. Contact information for BIODOC and other Belizean sources are listed in the Appendix.

The country—Belize is frequently compared to Massachusetts or El Salvador in size. It extends 280 km north–south and 109 km east–west, and comprises approximately 22,960 km^2. Belize shows a mosaic of zoogeographical affinities. Northeastern Belize, including Ambergris Caye, has very strong Yucatán Peninsula affinities. Coastal areas and cayes have Caribbean affinities. The western areas extending south to the Maya Mountains divide appear to have strong Petén affinities. The coastal pine/palm savannahs resemble Honduran pine areas to the south. With over 3050 mm of rain per year (Hartshorn et al. 1984), the southern Toledo District has the highest rainfall in the country and comprises yet another distinct area. The upper elevations of the Maya Mountains are perhaps among the more unique areas in Belize. Although not considered "highlands" by Guatemalan standards, the relative elevation difference from the lowlands suggests some affinities to highlands in Guatemala (B. W. Miller and C. M. Miller 1995).

Although selectively logged for 300 years, Belize is still sparsely populated (200,000 people) with approx-

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imately 70% of its land naturally vegetated (Wilson 1995). A network of protected areas constitutes about 20% of the country. Designations ranging from Forest Reserves to Nature Reserves, offer varying levels of protection. These factors offer a fairly intact and diverse avifauna to ornithologists, with a current bird checklist numbering 546. About 20% of these birds are neotropical migrant species, and of the breeding birds, 11% are regional endemics.

ECOLOGICAL AND BEHAVIORAL STUDIES

Resident species were the subject of several studies in Belize, many in the Gallon Jug (Orange Walk District) area. Willis (1960a) studied forest flocks and Willis (1960b) focused on foraging behavior of the Red-crowned and Red-throated Ant-Tanagers (*Habia rubica* and *H. fuscicauda*), and noted some differences in habitat and foraging. Other studies were on their courtship and territorial behavior (Willis 1960c) and nesting (Willis 1961). Lancaster (1964a, b) conducted life history studies on Slaty-breasted Tinamou (*Crypturellus boucardi*) in Gallon Jug. Verner (1961) studied the nesting behavior of the Red-footed Booby (*Sula sula*) at Half Moon Caye and described the flight behavior of this species (Verner 1965).

During the 1981 Royal Air Force Ornithological Society expedition to Belize, R. D. Powell looked at hummingbird communities and defense of flowers (Jenkins, unpubl. report). Species studied included Rufous-tailed Hummingbird (*Amazilia tzacatl*), Green-breasted Mango (*Anthracothorax prevostii*), and White-bellied Emerald (*Amazilia candida*). Data on nectar production for *Hamelia patens* at the Altun Ha archaeological site were also included. B. Miller and Tilson (unpubl. data) studied the comparative behavior of the Lesser Yellow-headed Vulture (*Cathartes burrovianus*), Turkey Vulture (*Cathartes aura*) and Black Vulture (*Coragyps atratus*) at Crooked Tree in 1983. Their observations (Miller and Tilson 1985) of kleptoparistism of Limpkins (*Aramus guarauna*) by Snail Kites (*Rostrhamus sociabilis*) were erroneously attributed to Clinton-Eitniear by Weyer (1984). Clinton-Eitniear studied the King Vulture (*Sarcoramphus papa*) in Belize over several years (Clinton-Eitniear and Weyer 1982).

Kamstra (1987) conducted ecological studies in the Cockscomb Basin with emphasis on determining the status and distribution of vegetation and fauna, particularly birds. Kamstra's checklist includes 280 species, including anecdotal records from previous observers. He gives abundance based on numbers of individuals encountered during each visit, seasonal status based on Weyer and Young (1983) and habitat associations based on seven broad vegetation types defined in his report. These studies took place during the dry season (January–April) 1986, and provided the first comprehensive examination of the Cockscomb Basin.

The Scarlet Macaw (*Ara macao*) is a species of conservation concern throughout its range. Barlow and Caddick (unpubl. report) compiled sightings of the Scarlet Macaw in Belize and Mallory (1993b) undertook the first ecological study here. The latter observations suggested that this species commutes between the Cockscomb Basin and the Chiquibul forest over a low pass. She estimates that in Belize there are only 30–60 birds.

Mallory and Brokaw (1997) studied the impact of selective tree cutting on birds and tree regeneration in the Chiquibul Forest Reserve, in the southern part of the country. Selective felling harvests more tree species than normal cutting regimes in order to promote regeneration and growth of commercial species while not endangering native plants and animals at a landscape scale. They looked at the impact of selective felling logging trials and noted changes in bird populations. Mallory and Brokaw (pers. comm.) also mist-netted and censused birds in riparian and upland forests in two areas of Belize: the Rio Bravo Conservation and Management Area in northwestern Belize and the Upper Raspaculo Valley in the south-central part of the country. Results from Rio Bravo suggested that the riparian forests were richer in birds, both resident and migrant species as well as numbers of individuals. This trend held true for the Upper Raspaculo Valley although sampling effort was less.

Baker (1996) suggested that over the last 20 years, the Orange-breasted Falcon (*Falco deiroleucus*) has been extirpated from Central America from all but Guatemala and Belize. The probable result is that these populations may be disjunct from the those in South America. Baker evaluated this species in Belize and we mapped its distribution and habitat

requirements for the National Protected Areas Management Plan (B. W. Miller and C. M. Miller 1995).

Behavioral studies currently in progress in Belize include C. Miller's unpublished observations on the life history and ecology of the Keel-billed Motmot (*Electron carinatum*) in Belize and Brown's (pers. comm.) study of lek behavior and correlates of male mating success in the White-collared Manakin (*Manacus candei*) at Bermudian Landing.

In the past 10 years, a number of neotropical migrant studies were carried out; one provided by an accidental opportunity. Eighty-six neotropical migrants were found dead on board a ship anchored off the coast of Belize City after a bout of bad weather occurring 4–7 October 1973. The ship's cook froze the specimens which were later examined in Amsterdam. Roselaar (1976) discussed differences between spring and autumn mass related to migration, and ageing criteria based on these specimens. Mills and Rogers (1990, 1992) reported studies of overwintering migrants in a large citrus plantation in central Belize during the winters of 1986–1987 and 1987–1988. The numbers and proportions of overwintering migrants were higher than previously reported from any other habitat on the Yucatán peninsula, but they concluded that citrus plantations were not suitable for all migratory species. Other wintering bird studies were conducted during 1988–1989 examining understory bird populations in five nonagricultural vegetation types to determine effects of disturbance and vegetation structure on migrant habitat use (Petit et al. 1992). In February 1990 Saab and Petit (1992) studied the impact of pasture development on bird communities and found that abundance of both resident and migrant birds was nearly 70% lower in grazed pastures compared with more structurally diverse abandoned pastures.

Belize was one of seven countries sampled over six winters by Robbins and coworkers (1992). Migrants were studied in a variety of managed arboreal habitats such as pine, cacao, citrus, and shade coffee plantations and were compared with those in extensive forest and isolated forest fragments. While certain species were present in relatively large numbers, other ground-foraging migrants were rarely found in the agricultural habitats. They concluded that intensive management might severely limit neotropical migrant use of some croplands subjected to overgrazing or heavy use of agricultural chemicals. Winter habitat studies assessment, using remote sensing, was carried out for the Wood Thrush (*Hylocichla mustelina*), in the Toledo District (Rappole et al. 1994).

Kricher and Davis (1992) sampled two disturbed sites and one undisturbed moist forest site in southern Belize near a Kekchi-Maya village. They concluded that habitat mosaics, including human-disturbed areas and successional forest, are important to maximize avian species richness, particularly when such habitats are directly accessible from mature forest. Although more than half of the species utilizing successional sites were edge species, mature forest was apparently essential to much of the avian species richness of disturbed sites.

DISTRIBUTION

Our understanding of species distribution since Russell's (1964) publication comes from several sources: museum specimen records, banding data, as well as published and unpublished expedition reports. Museum based data may provide many valuable records yet to be published. Although the primary value of specimen collections is for taxonomic research, they provide valuable information for synthesis and analysis of biogeographic patterns and habitat associations (Hathway and Hoagland 1993, Murray 1993). As we developed the Belize Biodiversity Information System (http://fwie.fw.vt.edu/wes/) in cooperation with the ministry of Natural Resources, we have been repatriating museum collection data. Although not exhaustive, our museum search has turned up additional information since Russell's (1964) monograph was published (Table 1). We would appreciate information on any collections not shown.

The two largest ornithological collections are maintained at the American Museum of Natural History (AMNH) and the British Museum of Natural History (BMNH). Both have specimens from Belize, but estimates of holdings are currently not available because neither is computerized. Having had a cursory look at both collections, we believe that developing a list of specimen records for Belize

TABLE 1. Museum holdings of Belize ornithological specimens.

Museum	Number of specimens
American Museum of Natural History	undetermined
British Museum of Natural History	undetermined
California Academy of Science	1
Carnegie Museum	3424
Coe College	Russell (1964)
Cornell University	50
Field Museum, Chicago	84
Louisiana State University, Museum of Zoology	Russell (1964)
Museum of Comparative Zoology	330+ see Russell (1964)
Philadelphia Academy of Science	Russell (1964)
Pomona College	Russell (1964)
Royal Ontario Museum	1236
University of Amsterdam Zoological Museum	86
University of California, Berkeley	3
University of Kansas	35
University of Michigan Museum of Zoology	964
University of New Mexico	31
U.S. National Museum	81
Yale Peabody Museum	1
Willamette University	Russell (1964)

will entail substantial time and effort for a species-by-species search.

Substantial collections were made by the Royal Ontario Museum in 1966 and 1969 at the archaeological site Altun Ha near Rockstone Pond (Barlow et al. 1969, Barlow et al. 1970) with additional collections made in 1971 in other areas of Belize (Barlow et al. 1972).

Russell (1964) summarized collections at the Carnegie Museum made by Blake and Agostini in 1926. Five collecting expeditions were made for the museum from 1971 to 1985 (Wood and Leberman 1987) and make up the largest recent collections known. Their Belize material consists of approximately 1700 study skins, 856 alcoholics and 865 osteological specimens (Parkes, pers. comm.).

Ornithologists use banding for many research objectives ranging from tracking local and migratory movements to long term population monitoring. We present a brief summary of banding efforts which provides one index of ornithological activity in Belize. There is no repository for banding data on resident species. Consequently, we have no means of assessing total numbers of birds banded other than the data provided by Robbins (pers. comm.), who assessed wintering bird habitat associations, and our own work. Therefore, the data supplied by the Bird Banding Laboratory (BBL) includes only those migrants and resident species approved for banding with BBL supplied bands.

The number of birds banded in the early 1960s approximates that of the mid 1980s (Fig. 1). The first peak represents the efforts of a one individual, Nickell, compared to the total number banded by six researchers in the 1980s. In fact, Nickell accounts for all but 125 of the more than 12,000 birds banded during the 1960s. Nickell (1968) set up eight netting stations in Stann Creek Valley, during six successive expeditions in March and April 1960–1965. His study was the first in Belize to look at Neotropical migrants on the wintering grounds with a 37% return on 10 species he banded. After Nickell, there are no banding records until 1969. Fewer than 200 birds were banded between 1969–1972 with a hiatus until 1982. The next wave of banding activity began in the 1980s which continues at various levels to the present time.

In the Stann Creek Valley, Rogers and Odum (1966) netted birds, but apparently did not band them, as part of a study on post- and premigration changes in mass. They compared premigratory mass buildup in Belize with post migratory mass for birds netted in Panama. They suggest that fat reserves in Gray Catbirds (*Dumetella carolinensis*), Orchard Orioles (*Icterus spurius*), Indigo Buntings (*Passerina cyanea*) and Common Yellowthroats (*Geothlypis trichas*) indicated that individuals attained trans-Gulf flight capabilities at different dates. Stann Creek Valley may have been the final stop in Central America before continuing north for some species.

The British armed forces, including the Royal Air Force Ornithological Society (RAFOS), the British Army Bird Watching Society (ABWS) and Royal Air Force Kinloss (RAFK), staged five ornithological expeditions to Belize from 1981 to 1989. All included netting and some banding. In addition to compiling sight records, these expedition re-

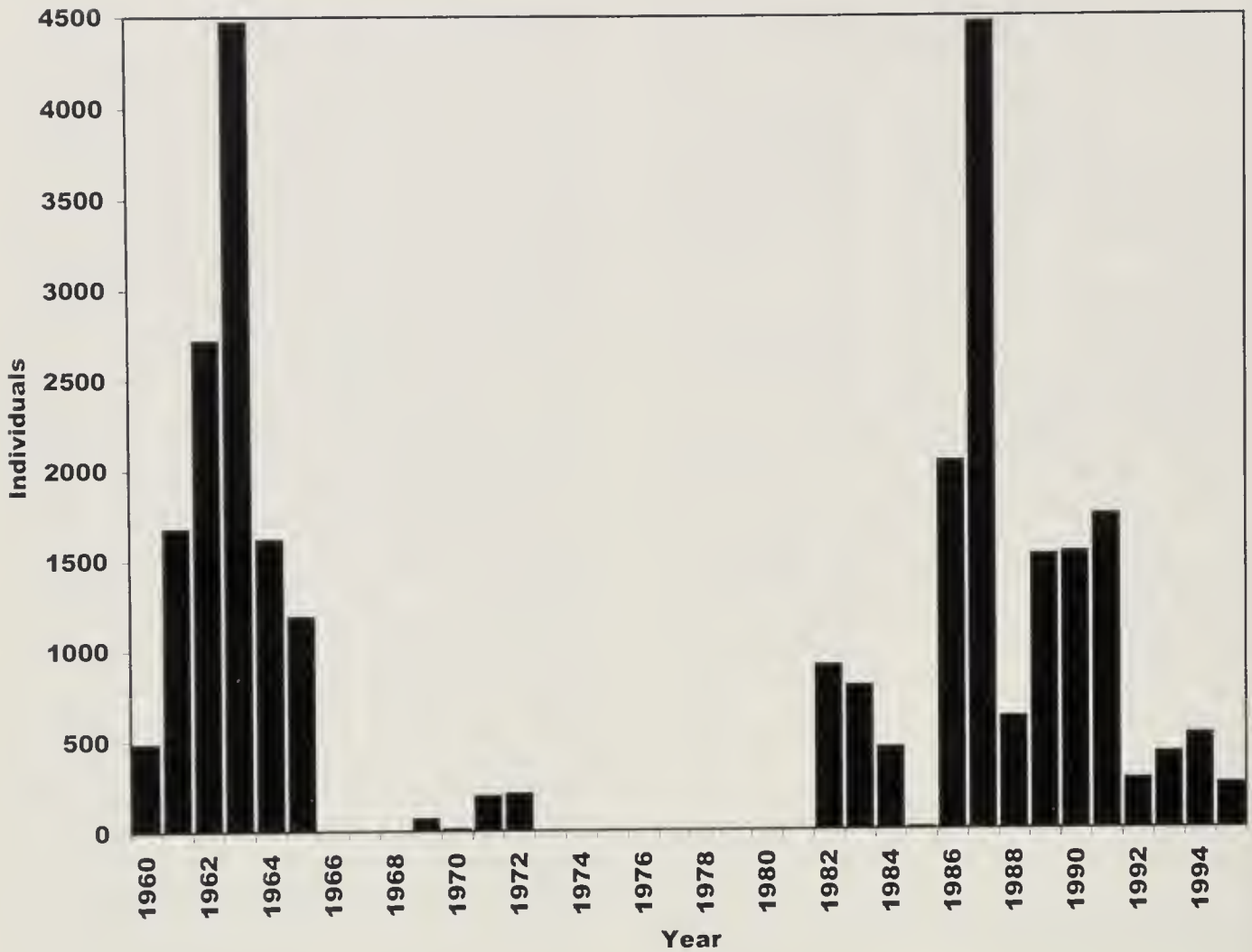

FIG. 1. Bird banding activity in Belize from 1960 to 1995 as indicated by number of Neotropical migrants banded. Data supplied by USGS-BRD Bird Banding Laboratory.

ports often included wing chord and mass for birds netted.

Jenkins (unpubl. report) compiled sight records and netting data for 107 species during the 1981 RAFOS expedition. Expedition dates were 24 February–10 April and include the following locations: Aguacate, Altun Ha, Belize City area, Big Falls Ranch, Caye Chapel, Guacamayo Bridge, Mountain Pine Ridge, Northern Lagoon, and Salamanca Camp/Jimmy Cut. Apparently they did not band any birds during this expedition although they recorded wing cord and mass for 584 birds netted. This report includes a summary of birds netted in 1979 in the Toledo District by members of the British Museum during studies of ectoparasites.

Hallchurch (1982) compiled sight records and netting data for 115 species during the 1982 ABWS expedition. He included a summary for 859 banded birds of the 1511 netted. Expedition dates were 23 February–16 March 1982 and include the following locations: Airport Camp, Altun Ha, Big Falls Ranch, Blue Creek, Toledo, and Guacamayo Bridge.

Counsell (unpubl. report) compiled sight records and netting data for 118 species during the 1986 RAFOS expedition. He included a summary of wing chord and mass for 1242 birds netted. Expedition dates were 28 February–18 March 1986 for Airport Camp, Big Falls Ranch, and Guacamayo Bridge.

We have so far been unable to locate a copy of the 1987 Royal Air Force Kinloss expedition report (Triggs 1987). However, Crease (unpubl. report) included data from that expedition showing 4375 birds netted, 2800 banded, and a total of 78 species. Crease (1990, unpubl. report) compiled sight records and netting data for 113 species during the 1989 ABWS expedition. He included a summary of wing chord and mass for 1977 birds netted. This report also includes information on recaptures of nine species of Neotropical

migrants banded by previous expeditions at Airport Camp and Big Falls Ranch. Expedition dates were 13 February–13 March 1989 and include the following locations: Airport Camp, Big Falls Ranch, Cockscomb Basin, Crooked Tree, and Guacamayo Bridge.

Wood and Adams (1985) documented the first Central American band recovery of a Blue-winged Warbler (*Vermivora pinus*). The bird was collected at First Hill along the Bladen Branch of the Monkey River and was originally banded in Kalamazoo, Michigan. Krichner and Davis (1986) studied wintering site fidelity of Neotropical migrants near Blue Creek, Toledo District, 1982–1984. They found high site fidelity in Kentucky Warblers (*Oporornis formosus*), Northern Waterthrush (*Seiurus noveboracensis*), Hooded Warblers (*Wilsonia citrina*), Gray Catbirds, and Wood Thrushes.

Published, unpublished, and gray literature provide substantial distributional information for Belize. Russell's (1964) monograph provided the basis for the first checklists for the country [Weyer and Young (1977), Weyer and Young (1983), Hartshorn et al. (1984)]. Russell (1966) also conducted follow up work in 1958, 1959 and 1963 in Belize and published distributional notes on the Black Rail (*Laterallus jamaicensis*) and Gray-breasted Crake (*Laterallus exilis*). Wood and Paulson (1988) added Couch's Kingbird (*Tyrannus couchii*) to the list of species recognized to occur in Belize. With the addition of this species, Tropical Kingbird (*T. melancholicus*) records should be reevaluated because rarely are these similar species differentiated in reports.

British military ornithological expeditions provided distributional records for select areas of Belize, many of which were related to military training exercises (Counsell and Etheridge 1986; Hallchurch 1982; Counsell, unpubl. report; Crease, unpubl. report; Jenkins, unpubl. report). In a number of cases these expeditions provided first records from remote sites such as Union Camp in the Maya Mountains. While valuable, these reports were the source of a few identification errors, some of which were perpetuated in subsequent literature. For example, the Northern Pygmy-owl (*Glaucidium gnoma*) was reported while netting and banding at the Guacamayo Bridge at the Macal River. This record was apparently accepted by Walters (1993) who published this and other records in a paper on first records for Belize. Howell (1995) refuted the validity of this and a number of other such records published by Walters (1993), e.g., Western Kingbird (*Tyrannus verticalis*), Cassin's Kingbird (*Tyrannus vociferans*), Hutton's Vireo (*Vireo huttoni*) and Western Wood-Pewee (*Contopus sordidulas*).

The Green-fronted Hummingbird (*Amazilia viridifrons*) record (Hallchurch 1982) is likely an error in identification also. Howell and Webb (1995) state that this species is resident in Mexico on the Pacific slope occurring in arid to semiarid scrub. Because the record from Blue Creek lies within a high rainfall area (Hartshorn et al. 1984), we speculate that this bird was more likely an Azure-crowned Hummingbird (*Amazilia cyanocephala*) which is similar in appearance and does occur in the area.

Another unlikely record was a Bald Eagle (*Haliaetus leucocephalus*) ". . . seen well by 10 members . . ." and ". . . another observer is familiar with the Golden Eagle (*Aquila chrysaetos*) and was able to exclude this as a possibility. . ." (Counsell, unpubl. report).

Weyer, a founding member of Belize Audubon Society, co-authored the first widely available checklists for Belize (Weyer and Young 1977, 1983; Wood et al. 1986). Weyer (1984) also presented the first records for Solitary Eagle (*Harpyhaliatus solitarius*), reported from the Macal River in the Mountain Pine Ridge Forest Reserve and included several other anecdotal reports on this species by others.

Another founding member of Belize Audubon Society and private pilot, W. F. Young undertook monitoring of Jabiru storks (*Jabiru mycteria*) in 1969 with annual aerial surveys of nesting through 1987. He provided locations of historical nesting sites (Young, pers. comm.), which we used to document that critical nesting habitat for this species fell largely outside the existing protected areas network (B. W. Miller and C. M. Miller 1995). Young also co-authored the first widely available checklist for Belize (Weyer and Young 1977, Weyer and Young 1983).

Five years (1987–1991) of study on habitat use of wintering Neotropical migrants by Robbins and Dowell contributed significantly

to the knowledge of Belize avifauna. Their work not only provided insights into habitat use by neotropical migrants but added a number of noteworthy records for Belize (Howell et al. 1992). Their 7540 species distribution records gathered throughout Belize were frequently the only records for some locations. Robbins and coworkers (1995) provided the first countrywide density distribution maps by habitat.

Brokaw and Lloyd-Evans (1987) provided the initial species list for the Bladen Nature Reserve and the first bird distribution records for that area of Belize. Mallory and Brokaw have provided records for the Rio Bravo Conservation and Management Area while working on long-term avian community ecology. In addition, Mallory (1991, 1993a) has contributed new distributional information from the upper Raspaculo River Basin in the Maya Mountains.

Parker added to the ornithological knowledge of the country during a brief study in a then little known area of the Columbia River Forest Reserve, now under logging concession. He found this area of wet forest and secondary growth unusually rich with at least 232 species representing well over 90% of the species restricted to evergreen forests in the country (Parker et al. 1993). Besides a number of wet foothill forest species [e.g., Violet Sabrewing (*Campylopterus hemileucurus*); Slaty Antwren (*Myrmotherula schisticolor*) a new country record; Speckled Mourner (*Laniocera rufescens*); and Shining Honeycreeper (*Cyanerpes lucidus*)] and a small component of montane forest species that typically occur in cloud forests [e.g., Spotted Woodcreeper (*Xiphorhynchus erythropygius*), Slate-colored Solitaire (*Myadestes unicolor*), and Common Bush-Tanager (*Chlorospingus opthalmicus*)], Parker characterized this forest as a very important staging ground for neotropical migrant passerines. Cerulean Warblers (*Dendroica cerulea*) were of particular note (Parker 1994) with more than 80 recorded in the tall hill forests.

Beginning in the mid-1980s, James used mist-netting and transects in various habitats in Belize including savannah areas, Rio Bravo Conservation and Management Area, and the Mussel Creek Drainage. He worked intensively at Bermudian Landing and recorded approximately 200 species (James, pers. comm.) during biodiversity surveys in an agricultural setting. He was also a participant in the Doyle's Delight expedition that documented higher elevation species such as Scaly-throated Foliage-gleaner (*Anabacerthia variegaticeps*), Spotted Woodcreeper, Common Bush Tanager, and Blue-hooded Euphonia (*Euphonia elegantissima*; Matola, unpubl. report). Besides Doyle's Delight, Matola has led several expeditions into remote areas of Belize over the past several years. Although primarily exploratory in nature, her observations and those of her colleagues have contributed to the ornithological knowledge of the country, particularly in the Toledo District. These areas include Dolores (Matola, unpubl. report) and the now besieged (by Malaysian loggers) Columbia River Forest Reserve where such species as the Slate-colored Solitaire, White-winged Tanager (*Piranga leucoptera*) and Common Woodnymph (*Thalurania furcata*) were notable (Matola, unpubl. report; Meadows et al., unpubl. report). An expedition into the Cockscomb Basin in 1990 included several sightings of the scarce Scarlet Macaw and secretive Agami Heron (*Agamia agami*; Matola, unpubl. report). A traverse across the Maya Mountains Divide offered distribution records in a little hunted area as well as commentary on unique vegetation types (Matola et al., unpubl. report). Matola has also co-authored a checklist for the country (Garcia et al. 1994).

McRae (unpubl. report) produced a comprehensive report for the zoological and site analysis for the National Protected Areas Management Plan, summarizing her observations of seabirds and coastal species during more than 13 years of residency on Caye Caulker. Her familiarity with Belize's barrier reef cayes and the coastal zone allowed her to pinpoint species (e.g., Wood Stork, *Mycteria americana*) and particular areas of conservation concern as well as add a new country record, the Northern Phalarope (*Phalaropus lobatus*) at Caye Rosario (McRae 1994). Her annually updated checklist for Caye Caulker provides some interesting migrant records (McRae, 1993) and may reflect trends over several years.

The Belize Audubon Society, founded in 1969, is more than a birdwatching society. BAS today functions as a leading NGO

charged by the government of Belize with management of six reserves. Its newsletter, which appears 3–4 times per year, is frequently cited. It offers conservation news, publishes field trip accounts and has served as an unofficial repository for bird records. The Belize Audubon Society also administrates two of Belize's three Christmas Bird Counts. Although the quality of the data gathered via Christmas Bird Counts (CBC) may be questionable (Arbib 1981, Bock and Root 1981), CBCs have tracked some interesting trends in Belize as the country develops. The first CBC was inaugurated in 1969 in an area near Belize City and covered 11 vegetation types including wetlands and riparian corridors along the Mussel Creek Drainage. In 1996, 21,501 birds of 181 species were counted with Tree Swallows (*Tachycineta bicolor*) and Blue-winged Teal (*Anas discors*) accounting for the high numbers (Craig 1997).

The second Belize CBC was begun in 1972 around the then new capital Belmopan, mainly in tropical forest of 12 recognized vegetation types. The count circle included a portion of the Hummingbird Highway which has undergone significant alteration over the years resulting from refugee settlement. Human settlement along the Hummingbird Highway has created a barrier between contiguous habitats (B. W. Miller and C. M. Miller 1995). Data from this CBC may track changes in relative abundance for this rapidly developing section of the country. The 1996 count recorded 4546 birds of 198 species (Craig 1997).

In 1990, the Gallon Jug CBC began in northwestern Belize on private property which contains nine vegetation types and an agricultural area surrounded by approximately 400,000 ha of tropical forest. The 1996 count resulted in 2823 birds of 217 species (Craig 1997). Combined, all three CBCs covered 26 vegetation types.

We began ornithological study in Belize in 1986 with inventory work along the Mussel Creek Drainage, a critical wetland habitat. Five years of ornithological inventories combined with other biodiversity studies at the Maya archaeological site, Caracol, led to the establishment of the Chiquibul National Park in 1991. Distribution and life history studies of the little known Keel-billed Motmot were conducted simultaneously (C. M. Miller 1991, 1994; B. W. Miller and C. M. Miller 1996). We also assisted in Robbins' wintering bird survey in 1987 and 1991, and evaluated Black Catbird (*Melanoptila glabrirostris*) populations on Caye Caulker (B. W. Miller and C. M. Miller 1991).

At the request of the Belize Audubon Society and the Forest Department, we conducted avian inventory work at many sites throughout the country deemed of conservation concern. We have produced many unpublished technical reports, popular articles and publications, and checklists (B. W. Miller and C. M. Miller 1998), broadening the knowledge of species distributions within the country. We began to evaluate avian distributions in the country (B. W. Miller and C. M. Miller 1992) as we developed a natural history database to compile distribution records across the country with emphasis on 78 areas of concern for a zoological and site analysis for the National Protected Areas Management Plan (B. W. Miller and C. M. Miller 1995).

PROBLEMATIC SPECIES REQUIRING VERIFICATION IN BELIZE

Certain species tend to appear repeatedly in lists, expedition accounts, and anecdotal reports. Their presence or absence can be difficult to verify. Howell and Webb's (1995) guide to birds of Mexico and northern Central America has clarified many questions but certain species remain problematical.

Cinnamon Teal (Anas cyanoptera).—Not shown by Howell and Webb (1995), but record from Big Falls Rice Station, along the Belize River (Counsell and Etheridge 1986).

Masked Duck (Oxyura dominica).—Not shown for Belize by Howell and Webb (1995); however, anecdotal records exist from birding groups. Recorded during the 1985 Belize City CBC.

Solitary Eagle (Harpyhaliaetus solitarius).—Not shown by Howell and Webb (1995), but many records (Weyer and Young 1983; Weyer 1984; Clinton-Eitniear 1986; Kamstra 1987; Meerman and Williams, unpubl. report) within Belize.

Swainson's Hawk (Buteo swainsoni).—Howell and Webb (1995) state this species requires verification. We have several reports of the species but lack proper documentation.

Harpy Eagle (Harpia harpyja).—Persistent

sightings occur with some regularity (Weyer 1984, Dunham 1994) although the large similar sized Crested Eagle (*Morphnus guianensis*) also has been documented in Belize and the birds may be confused by observers. Historical Harpy Eagle records were noted during a time when the Crested Eagle had not yet been documented in Belize and the available field guides either had no plates (e.g., Blake and Tibbits 1953) or did not list the Crested Eagle (Peterson and Chalif 1973). Howell and Webb (1995) show the Harpy Eagle for the southern part of the country; we believe verification is still needed.

Crested Caracara (Caracara plancus).—Not shown for Belize by Howell and Webb (1995), but isolated anecdotal reports persist in the northern part of country.

Yellow-breasted Crake (Porzana flaviventer).—One unverified record from Monkey Bay Sanctuary in the Belize District exists. Howell and Webb (1995) state that the Wood and coworkers' (1986) report requires verification.

Long-billed Dowitcher (Limnodromus scolopaceus).—Howell and Webb (1995) state "possibly Belize." There are a few recent anecdotal records for this species.

Forster's Tern (Sterna forsteri).—Only one record of this species from Ambergris Caye in 1994 from a qualified observer. Howell and Webb (1995) state there are no verified records from Belize and that it is not common in Belize as reported by Wood and coworkers (1986).

Crested Owl (Lophostrix cristata).—Added to the Belize list (B. W. Miller and C. M. Miller 1992); Parker and coworkers (1993) extended the known range.

White-throated Swift (Aeronautes saxatilis).—Several recent reports for Belize; however, Howell and Webb (1995) say that it needs confirmation. This is a species that may be confused with other Swifts.

Blue-throated Goldentail (Hylocharis eliciae).—Included by Russell (1964) as unconfirmed. Mills and Rogers (1988) mist-netted an individual in a citrus orchard off the Western Highway. Platt (unpubl. report) listed the species as "probable" during wildlife surveys in the Orange Walk District. Howell and Webb (1995) show this species in the southern part of the country only.

Paltry Tyrannulet (Zimmerius vilissimus).—Howell and Webb (1995) say this species requires verification. A record exists from Parker and coworkers (1993) and there are anecdotal records from the Rio Bravo and Gallon Jug areas in the Orange Walk District.

Cassin's Kingbird (Tyrannus vociferans).—There are a few records for Belize in the northern part of the country: Cox Lagoon and Shipstern Nature Reserve (Hunt and Tamarack, unpubl. report; Meerman 1993), as well as during the Belize City CBC in both 1985 and 1986. BBL records show three birds banded each year in 1960, 1961, and 1962, and four in 1963 and in 1985. Howell and Webb (1995) state that the species requires verification in Belize.

Warbling Vireo (Vireo gilvus).—Robbins (pers. comm.) first documented this species in Belize during wintering bird surveys January 13, 1988. Parker recorded the species in the Columbia River Forest Reserve (Parker et al. 1993). Howell and Webb (1995) do not list the species for Belize.

Orange-crowned Warbler (Vermivora celata).—Howell and Webb (1995) report that this species is possible for Belize. Records for it include Bermudian Landing (James and Bider, pers. comm.) and Crooked Tree (Counsell and Etheridge 1986). It was also reported during three CBCs: Belize City in 1976 and 1977, and Belmopan in 1983.

Tropical Parula (Parula pitiayumi).—Recorded at Columbia Forest Reserve (Parker et al. 1993); one mist-netted and photographed at Caracol (Miller and Miller, unpub. data). Howell and Webb (1995) state that the species requires verification.

Hermit Warbler (Dendroica occidentalis).—Howell and Webb (1995) show no records, but reported at Bermudian Landing (James and Bider, pers. comm.).

Blackpoll Warbler (Dendroica striata).—Although Howell and Webb (1995) do not list the species for Belize, three unverified records exist in the country: Caye Caulker (McRae 1993), Rio Bravo and Gallon Jug.

Flame-colored Tanager (Piranga bidentata).—Howell and Webb (1995) do not list it for Belize, but recently reported for the country by reliable observers (M. Meadows, pers. comm.; L. Jones, pers. comm.) near Over-the-Top, Cayo District.

Lazuli Bunting (Passerina amoena).—Howell and Webb (1995) do not list it for Belize. One record exists from a reliable observer along the Macal River, Chiquibul National Park where several individuals were seen during a four day period in 1993 (Tzib, pers. comm.).

Audubon's Oriole (Icterus graduacauda).—Not listed for Belize by Howell and Webb (1995); however, records exist for Gallon Jug and Rio Bravo, as well as Lamanai (Noble et al., pers. comm.) and the Bladen (Brokaw and Lloyd-Evans 1987). Robbins (pers. comm.) recorded two individuals in the Toledo District in January 1989.

AREAS FOR FUTURE STUDY

Since the 1960s, Belize has developed a solid conservation record. Within the past 10 years, the country has attracted increasing numbers of researchers and student groups in the natural sciences including ornithology. Even so, there is clearly still a need for additional ornithological work in Belize including baseline inventories, long term monitoring, and species specific population estimates for species of conservation concern.

We evaluated the status of the protected areas coverage for species of conservation concern and compiled data on bird distributions (B. W. Miller and C. M. Miller 1995). Many areas of the country are well known but others are less so. Ironically, many readily accessible areas are still poorly known. The allure of new discoveries in remote areas such as the Bladen Nature Reserve, the Columbia River Forest Reserve, Little Quartz Ridge and the Upper Raspaculo River Basin has attracted a number of expeditions (Brokaw and Lloyd-Evans 1987; Iremonger and Sayre 1994; Mallory, pers. comm.; Meadows et al., pers. comm.; Parker et al. 1993). Consequently, baseline data for these areas is more complete than many more accessible areas of the country.

We have mapped known species numbers by topographic quadrant (Fig. 2). These numbers reflect areas of survey activity and areas where knowledge gaps exist, and are not intended as a measure of true species richness. Quadrants with low numbers indicate areas where baseline avian inventory work is necessary for a more complete understanding of species distributional limits within Belize. There are many protected areas with scant baseline data while others have relatively abundant information. We suggest that those interested in making contributions to the ornithological knowledge of Belize contact either the Conservation Division of the Forest Department, Ministry of Natural Resources, or Belize Audubon Society (see Appendix) to inquire about current priorities. This could help eliminate duplication of effort and channel research interests into areas most needing attention.

SPECIFIC AVIAN CONSERVATION CONCERNS IN BELIZE

At the conclusion of the zoological and site analysis (B. W. Miller and C. M. Miller 1995), several species and families were considered in need of further study. Most of these face threats from habitat conversion or other human induced impacts.

The status of many of Belize's seabird colonies is unclear. McRae (1994) suggests that many may be at risk with the acceleration of coastal and offshore development bringing with it increased tourism and pollution. A comprehensive survey of the coastal and offshore islands during the nesting season would provide a better picture of the status of these species. Although habitat loss from ever-increasing development pressures on Belize's offshore islands continues to threaten seabird colonies, introduced species are another insidious threat. The introduction of *Rattus rattus* to Half Moon Caye Natural Monument (NM), 80 km east of Belize City, is such an example. Half Moon Caye NM is the site of a mixed colony of thousands of Red-footed Boobies and Magnificent Frigatebirds (*Fregata magnificens*). An early naturalist who collected in Belize's cayes (Salvin 1864) discussed the colony but did not mention the presence of *Rattus rattus,* although Verner (1961) did. A five year management plan calls for a rat eradication program and monitoring of this colony that is quite likely impacted by the rat. Another potential impact to the colony is increased tourist visitation.

The Jabiru is at risk from habitat disruption and this charismatic species is of high touristic interest. Unfortunately, the Jabiru apparently does not tolerate repeated disturbance and at

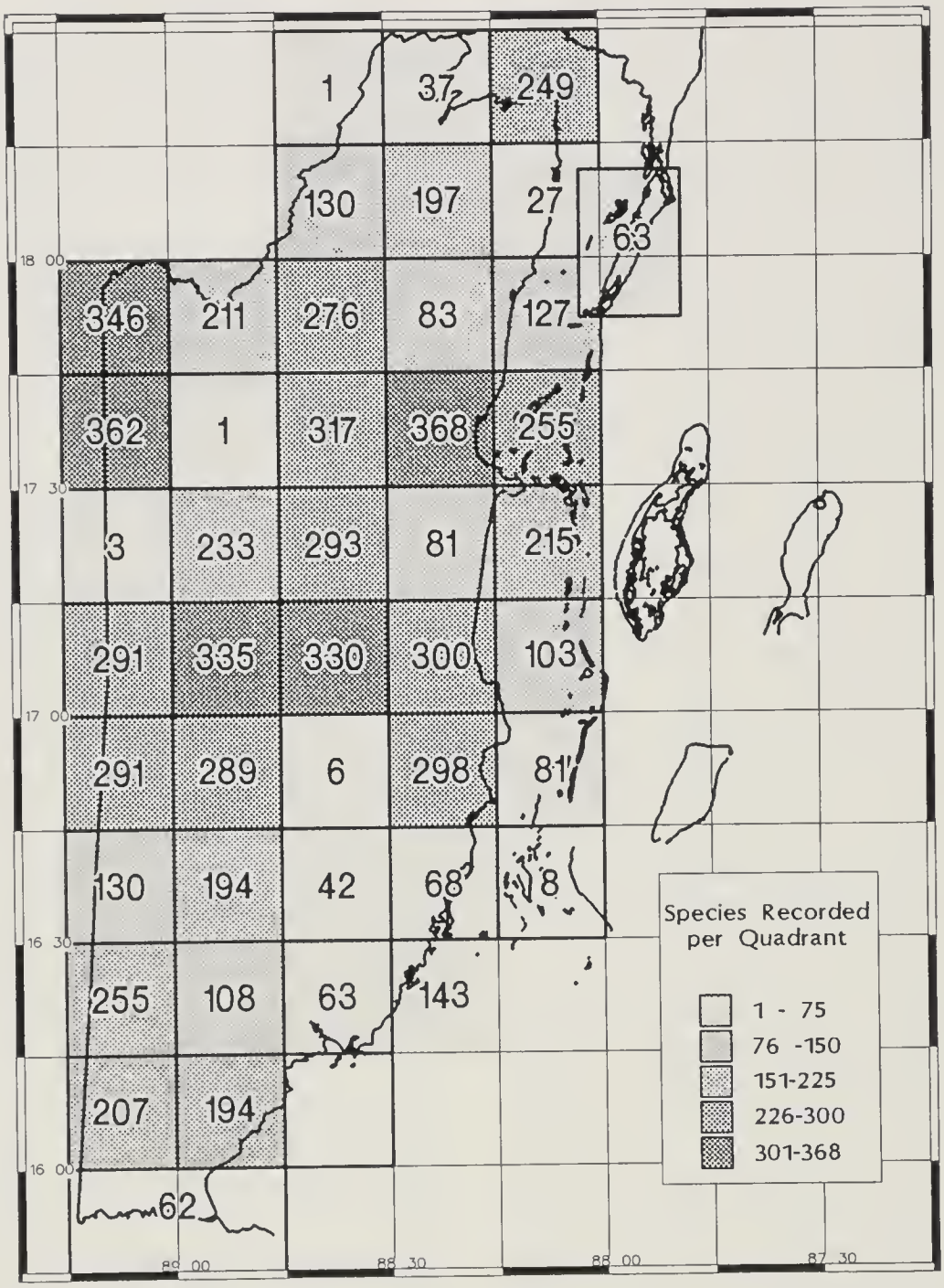

FIG. 2. Number of avian species per topographic quadrat in Belize.

least two nests failed in 1994, possibly as a result of tourist visitation. This species migrates from the Usumacinta drainage (Howell and Webb 1995) and arrives in Belize around October to nest. As marsh forests have been cleared for upland rice in the northern part of the country, the resulting shallow wetlands may provide increased foraging opportunities for the Jabiru. It may return to the same nest sites year after year, most of which are outside of the existing protected areas (B. W. Miller and C. M. Miller 1995). A monitoring program for this species would be useful.

The Crested Guan (*Penelope purpurescens*) and the Great Curassow (*Crax rubra*) are game birds legally hunted in Belize. However, there is growing concern about sustainability of this practice as well as conservation of the species. The Chief Conservation Officer has expressed interest in proposing regulations on take (R. Manzanero, pers. comm.). We suggest that population estimates and the impact of hunting on these species (see Silva and Strahl 1991) would give the Conservation Department the information it needs to impose limits and seasons on these species.

The Ocellated Turkey (*Meleagris ocellata*) is a regional endemic with one of the most restricted ranges of all gallinaceous birds in the Americas (Gonzalez et al. 1996). It has been a species of conservation concern for some time (Collar and Andrew 1988, Mountfort and Arlott 1988). Its distribution in Belize includes formally protected areas and large parcels of private land where hunting is not permitted or is at least curtailed. Because it appears locally abundant, the species was assumed to be secure and Collar and coworkers (1992) did not include it as a species of concern. Although it is not legally hunted in Belize the turkey is taken opportunistically. In a recent study in Tikal National Park, Guatemala, Gonzalez and coworkers (1996) showed that survival rates for hens ranged from 60% to 75% and poult survival was 13% during the two year study. With growing immigrant populations, subsistence hunting in Belize may have long term implications for the Ocellated Turkey. Gonzalez and coworkers (1996) found that 67% of subsistence hunters in the Tikal area hunted Ocellated Turkey. We suggest that investigation on the impact of hunting, mapping distributions, and developing countrywide population estimates for the Ocellated Turkey would provide important data for this species' management.

Parrots in the local pet trade are a matter of concern. Apparently there is some evidence that the regional endemic Yellow-headed Parrot (*Amazona oratrix belizensis*) is being exploited for foreign markets (Somerville 1997). Habitat loss is another concern. The Conservation Department has indicated interest in addressing this problem (R. Manzanero, pers. comm.) with a captive bird registering scheme for management purposes. Baseline population data for monitoring of this species and other *Amazonas* would be valuable. More than 60 Scarlet Macaws were counted by wardens near the village of Red Bank where macaws have recently been heavily poached (Saqui 1997). Conservation research for this northern Central American subspecies (Weidenfeld 1994) and other parrots is badly needed.

The Black Catbird is restricted to the east coast of the Yucatán, Cozumel Island and northeastern Belize (Phillips 1986). It is at risk because of habitat loss resulting from increased development, both in Mexico and Belize. To date, nesting in Belize is documented only from Caye Caulker (McRae, pers. comm.) and Shipstern Nature Reserve (Meerman, pers. comm.). In 1991, the species was considered under threat on Caye Caulker and by 1993 substantial habitat had been lost (B. W. Miller and C. M. Miller 1991, 1993). Anecdotal reports suggest it may nest on northern Ambergris Caye but this needs to be verified. Studies to determine its status and range beyond Caye Caulker would be useful.

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APPENDIX: SOURCES OF GRAY LITERATURE

A check to cover copy costs and postage accompanying literature requests from any of these sources would be appreciated.

Belize Audubon Society, P.O. Box 1001, Belize City, Belize, Central America, E-mail: base@btl.net

BIODOC, Centro De Documentacion En Vida Silvestre, Universidad Nacional, Heredia, Costa Rica, Central America, E-mail: biodoc@irazu.una.ac.cr; Internet: http://www.una.ac.cr./biodoc

Conservation and Environmental Data System (CEDS), Land Information Centre, Ministry of Natural Resources, Belmopan, Belize, Central America

Forest Department, Ministry of Natural Resources, Belmopan, Belize, Central America

Programme for Belize, P.O. Box 749, Belize City, Belize, Central America, E-mail: pfbel@btl.net

Wilson Bull., 110(4), 1998, pp. 559

THE QUETZAL AND ITS CONSERVATION IN THE MEXICAN SOUTHEAST

MARÍA DE LOURDES AVILA HERNÁNDEZ[1]

Mexico is one of the 10 nations with the greatest biodiversity and Chiapas may be the state with the greatest variety of natural resources, including 19 vegetation types, more than 8500 species of higher plants, 1200 species of butterflies, 92 species of amphibians (38% of all Mexican species), 229 reptiles (32%), 642 species of birds (66%), and 180 species of terrestrial mammals (36%). Chiapas is also the state with the most formally-established habitat preserves: 24. Of these, three biosphere reserves stand out: Montes Azules, Lacantún, and El Triunfo. The latter protects the last remnants of Mexican cloud forest in which live the Resplendent Quetzal (*Pharomachrus mocinno*) and the Horned Guan (*Oreophasis derbianus*), which is endemic to Chiapas and neighboring Guatemala. I have studied the quetzal in El Triunfo since 1986, first its biology and distribution and later its migration. These studies have clearly shown the need to reorient conservation measures for the quetzal in Mexico. Because the quetzal migrates to lower altitude tropical forests, conservation areas are not sufficiently large to protect the quetzal, demonstrating the need to develop natural corridors among reserves. The relationship between certain plants and the quetzal is of special interest in lower elevation zones, where increasing human disturbance is principally affecting vegetative cover. These studies provide a basis for the protection of the quetzal and other species elsewhere in Mexico.

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México es uno de los 10 paises de mayor biodiversidad, y Chiapas es quizás el estado que presenta la mayor variedad de recursos naturales, por ejemplo 19 tipos de vegetación, más de 8500 especies de plantas superiores, más de 1200 especies de mariposas diurnas, 92 especies de anfibios (38% de los de México), 229 de reptiles (32%), 642 especies de aves (66%), y 180 especies de mamíferos terrestres (36%). Chiapas es también el estado con mayor cantidad de áreas naturales protegidas formalmente establecidas: 24 en total, de estas sobresalen tres reservas de la biósfera, Montes Azules, Lacantún, y El Triunfo. Esta última protege los últimos reductos de bosque de niebla de México en donde habitan además del Quetzal el Pavón (*Oreophasis derbianus*), ave endémica de Chiapas y Guatemala. He investigado el quetzal en El Triunfo desde 1986, primero sobre su biología y distribución y posteriormente sobre su migración. Estos estudios han mostrado claramente la necesidad de reorientar las medidas de conservación de esta especie en México, porque el quetzal migra hacia selvas tropicales de menor altitud. Las unidades de conservación no son suficiente grandes como para proteger el quetzal, mostrando la necesidad de fomentar corredores naturales entre unidades de conservación. La relación entre algunas plantas y el quetzal cobra especial interés en zonas bajas en donde cada vez es mayor la presión humana, afectando principalmente a la cobertura vegetal. Se pueden considerar estos estudios como base para la protección del quetzal y otras especies en otros lugares de México.

Short Communications

Wilson Bull., 110(4), 1998, p. 560

Attempted Kleptoparasitism of Ospreys by Great Blue Herons

John R. Squires[1,2]

ABSTRACT.—Two attempts of kleptoparisitism of Ospreys (*Pandion haliaetus*) by Great Blue Herons (*Ardea herodias*) were observed in Grand Teton National Park, Wyoming. Two herons vocalized and bill thrusted at Ospreys as they emerged from the water following dives for fish. Although both attempts were unsuccessful (the Ospreys failed to capture a fish), the intensity of the attacks suggest that Great Blue Herons may be capable of taking fish from Ospreys. *Received 12 Nov. 1997, accepted 2 June 1998.*

On 25 April, 1989, while observing Trumpeter Swans (*Cygnus buccinator*) on the Snake River in Grand Teton National Park, Wyoming, I observed kleptoparisitism attempts of Ospreys (*Pandion haliaetus*) by Great Blue Herons (*Ardea herodias*). Great Blue Herons take prey from gulls and shorebirds and fish from Osprey nests [Butler, R. W. 1992. Great Blue Heron. *In* The birds of North America, no. 25. (A. Poole, P. Stettenheim, and F. Gill, Eds.). The Academy of Nat. Sci., Philadelphia; The American Ornithologists' Union, Washington D.C.]. However, observations of direct kleptoparasitism on Ospreys by Great Blue Herons have not been reported. On 25 April, I observed two Ospreys hunting behind Jackson Lake Dam on the Snake River. As one Osprey dove into the water, a Great Blue Heron that was perched in a nearby tall conifer flew to the spot where the Osprey was briefly submerged. As the Osprey emerged from the water and tried to become airborne, the heron briefly hovered (similar to landing on nests) within 0.5 m of the hawk while vocalizing and thrusting its bill presumably in an attempt to force the hawk to drop any prey it may have captured. The Osprey, unsuccessful in catching a fish, flew rapidly in a zigzagged pattern down the river to evade the heron. The heron followed the Osprey for approximately 5 m before both birds left the area in different directions. Within a few minutes, a second Osprey plunged into the water in the same general area and a second heron, which was perched in a different conifer along the river, tried to force the Osprey to drop prey as described above. Although both attempts were unsuccessful, the intensity of attacks by these herons suggests that sometimes they are successful in taking prey from Ospreys.

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The First Record of Burrowing Owls Nesting in a Building

Ricardo Zambrano[1]

ABSTRACT.—A nuisance owl complaint resulted in the discovery of a Burrowing Owl (*Athene cunicularia*) nesting in a dormer of a house in Davie, Florida. Burrowing Owls have been reported nesting in artificial nest boxes, pipes, and culverts but this is the first published report of nesting in a building. One adult and one downy chick were observed on the first two visits. Two adult sized birds were observed on the last visit. It is believed that wet conditions and unsuitable

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soil types in the area provided the impetus for the shift from ground to structure nesting. *Received 7 Jan. 1998, accepted 3 June 1998.*

Burrowing Owls (*Athene cunicularia*) typically nest underground in burrows excavated by other animals or dig their own. Instances of above ground nesting (Cavanagh 1990) and nesting in artificial structures such as concrete pipes, culverts, and under sidewalks have been observed (M. Robson, pers. comm.). Artificial underground nest boxes used in passive relocations also have been used for nesting (Trulio 1995). Other species of owls, notably the Barn Owl (*Tyto alba*), regularly use buildings for nesting; however, this is the first published report of Burrowing Owls successfully nesting in a building.

A complaint from a home owner having roof repairs led to the discovery of a Burrowing Owl nest on 22 May 1997 in western Davie, Broward County, Florida. An adult Burrowing Owl was observed perched on the roof of the house. Feces and pellets were visible outside a triangular opening on the side of a dormer. One downy chick was observed and heard inside the crevice between the walls. I inspected the nest again on 9 June. At this time an adult was on the roof and I heard a chick calling. Two adult-sized birds were observed near the entrance hole on 8 July. One bird was slightly smaller and did not stray far from the nest entrance when approached; but I was unable to determine if it was a fledged young or an adult.

Although only one adult was observed during the first two visits, the home owner reported having seen a pair prior to the roof repairs. What is presumed to be the same pair was also observed nesting on the property the previous year by the home owner. The burrow was underground and adjacent to the house. The nest is thought to have failed as no young were observed. Burrowing Owls in Florida prefer sandy, well-drained areas with short herbaceous ground cover (Millsap 1996). However, western Davie is a former freshwater sawgrass (*Cladium jamaicense*) marsh drained to create cattle pastures and residential developments. Flooding and trampling of burrows by cattle are the primary causes of known nest failures in this area (Mealy 1997). Not surprisingly, there are few records of Burrowing Owls nesting in western Davie (Runde and Reynolds 1990). Wet conditions and unsuitable soil types on the property and the surrounding area might have forced the owls to use the dormer as a nesting burrow. The use of structures for nesting has also been reported in some species of terns and skimmers, especially in areas where suitable nesting habitat is limited or marginal (Fisk 1978, Smith 1996, Zambrano et al. 1997). Faced with intense agricultural practices and development of their nesting habitat (Millsap 1996), Burrowing Owls might similarly be exploiting alternative nesting substrates in otherwise unsuitable habitat.

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Incestuous Behavior in Spotted Owls

Peter C. Carlson,[1,4] William S. LaHaye,[2] and Alan B. Franklin[3]

ABSTRACT.—Inbreeding of closely related individuals can be referred to as incest, generally limited to parent-offspring or sibling pairs. Cases of incest in raptors are rarely reported because they require long term monitoring of marked individuals. We documented 3 cases of close inbreeding among 730 pairs of individually marked Spotted Owls (*Strix occidentalis*) across all 3 subspecies during 14 years of study. The incestuous pairings we observed may be the result of shorter than normal dispersal distances and chance encounters. Although the level of incest appears to be low in Spotted Owls, the level of actual inbreeding remains unknown. *Received 7 Jan. 1998, accepted 11 June 1998.*

Incest is extreme inbreeding of closely related individuals as in parent-offspring or full sibling pairs (Shields 1993). Incest in raptor species has been documented but appears to be quite rare. Six cases of incest have been reported among Barn Owls (*Tyto alba;* Petty et al. 1986, Shaw and Dowell 1989, Taylor 1994, Roulin 1996) and four cases for a Burrowing Owl (*Athene cunicularia*) population (Millsap and Bear 1990). We also found one case reported for each of the following species: Screech Owl (*Otus asio*; Van Camp and Henny 1975), Merlin (*Falco columbarius*; James et al. 1987), Osprey (*Pandion haliaetus*; Postupalsky 1989), and Spotted Owl (*Strix occidentalis;* Gutiérrez et al. 1995). Rosenfield and Bielefeldt (1992) reported a pairing between a female Cooper's Hawk (*Accipiter cooperii*) and her grandson, which is another example of close inbreeding. The relatedness of the individuals can be represented by the coefficient of relationship, r (Wright 1922). We use $r \geq 0.5$ (e.g., mother-son or full sibling pairs) to define incest and define $r \geq 0.25$ (e.g., grandmother-grandson or half-sibling pairs) as close inbreeding. Inbreeding depression can be a cost of close inbreeding while inbreeding avoidance may reduce the cost; these mechanisms are difficult to document in wild populations (Pusey and Wolf 1996).

Detection of close inbreeding requires long-term monitoring of marked individuals. Here we report two cases of incest and one case of inbreeding by half-siblings from five Spotted Owl demographic studies that cover all three subspecies (*S. o. occidentalis, S. o. caurina,* and *S. o. lucida*). The studies were located in northwestern California (Klamath Mountains), central California (Sierra Nevada), southern California (San Bernardino Mountains), Arizona (Coconino Plateau), and New Mexico (Tularosa Mountains). In these studies, individuals were marked with both uniquely numbered U.S. Fish and Wildlife Service (USFWS) aluminum leg bands and color bands (Forsman et al. 1996). These five studies span 14 years and involve 730 pairs with both individuals uniquely marked (for details on sexing, capturing and banding, see Franklin et al. 1996). We examined all pairings of known individuals for incestuous relationships across all studies and years. We include a half-sibling pair because it illustrates the potential dispersal patterns associated with inbreeding. We assumed that observed parents were the biological parents. Extra-pair copulation may occur in Spotted Owls, but it has not been documented (Gutiérrez et al. 1995).

We observed the first case of incest in the San Bernardino Mountains in southern California. This study began in 1987 and included the entire mountain range (1890 km^2) encompassing the local insular Spotted Owl population (LaHaye et al. 1994). In 1991, we located a female paired with her male offspring. The female was originally banded as an adult in 1990. She nested and fledged one young that year. In 1991, she was located in a different

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territory where she was seen copulating with a banded subadult male on 1 May. The male was recaptured on 14 May 1991 and determined to be the female's offspring from the previous year. The male had dispersed 5.3 km from his natal nest site. The birds were confirmed to be nesting but failed to fledge young.

The case of close inbreeding occurred in the San Bernardino Mountains in 1995 when a pair of half-siblings were located together. The female and male fledged in 1990 and 1992, respectively, from different nests in the same territory and shared the same mother. Each of the half-siblings had nested and fledged young with different mates prior to 1995. The male was first recaptured as an adult in 1994 and remained on the same territory through 1996. The female was recaptured in 1991 as a nonterritorial bird. She was rebanded with a unique color band and was resighted in 1992 and 1994 on a different territory before joining her half-brother on 16 May 1995. They were observed nesting 8.4 km from their natal nest sites and fledged two young. They remained paired but did not fledge young in 1996. Because the female made several movements between territories, of 13.0, 16.8, and 3.5 km respectively, we suspect that this pairing was a chance occurrence.

The second case of incest occurred in northwestern California near Willow Creek in 1997. This study began in 1985 and encompassed 2076 km^2 (Franklin et al. 1996). On 24 July 1997, we located a pair of previously banded owls with one fledgling. Upon recapture, both adults were determined to be siblings from the same nest. They had been banded in June 1994, and were located 10.6 km from their natal nest site. No owls were located at this site prior to 1997 and this was the first time these siblings were detected since 1994.

We have not observed any incest in the study areas in central California, Arizona, or New Mexico. This may be due to smaller sample sizes on these study areas as a result of both smaller geographic extent and shorter study periods.

It is unusual to find siblings associated with each other after they begin dispersing. In northwestern California, fledglings tend to disperse in random directions, and females typically move farther than males (for 33 females and 44 males, $\bar{x} \pm$ SD: 23.5 ± 17.4 km vs 17.4 ± 19.1 km; Gutiérrez, pers. comm.). The siblings and half-siblings reported above all dispersed less than the average, increasing the chances of pairing. This is similar to the dispersal behavior of the Merlin pair reported by James and coworkers (1987). Thus, we suspect that the sibling pairs were a result of both dispersal behavior and chance occurrence.

Although quite rare among Spotted Owls, incest occurs occasionally and appears to be a chance occurrence. The short dispersal distance of the incestuous birds may be a factor. Although inbreeding avoidance can account for dispersal patterns (Pusey 1987), we do not know if this explains the dispersal behavior of Spotted Owls. The previously reported case of incest in Spotted Owls was for a father-daughter pair in Oregon where the female did not disperse from her natal site (Gutiérrez et al. 1995). The proportion of cases (2 of 730) is fewer than that reported for a population of Barn Owls (2 in 130 pairs; Roulin 1996) and similar to that reported for Barn Owls in Scotland (1 in 157 pairs; Taylor 1994) and for the Mute Swan (*Cygnus olor*; 7 cases in 1389 pairs; Coleman et al. 1994), which is one of the few long-lived avian species with extensive data on mated pairs. We do not know how inbreeding may affect Spotted Owl populations. The San Bernardino Mountain population is of particular interest because it is geographically isolated and the chance for random matings resulting in inbreeding should be greater. Although incest appears to be rare in Spotted Owls, the level of inbreeding remains unknown.

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Red-cockaded Woodpeckers Ensnared in Mesh Snake Traps

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ABSTRACT.—The Red-cockaded Woodpecker (*Picoides borealis*) is a federally endangered cavity nesting species. Mesh snake traps are placed near the base of cavity trees to prevent tree climbing and potential nest predation by rat snakes. In 1997, we documented one live and four dead Red-cockaded Woodpeckers ensnared in mesh snake traps at the Bienville National Forest and Noxubee National Wildlife Refuge, Mississippi. *Received 21 Nove. 1997, accepted 11 June 1998.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a federally endangered species that inhabits mature, open pine forests throughout the southeastern United States (Jackson 1994). Red-cockaded Woodpeckers excavate cavities in live pines for roosting and nesting. Suitable cavity sites are limited (Copeyon et al. 1991), and populations are declining throughout the species' range (James 1995). Intensive management techniques, such as midstory removal, cavity entrance restrictors, artificial cavity inserts, and mesh snake traps have been used to promote recovery of the species (Copeyon 1990, Richardson and Stockie 1995, Raulston et al. 1996). Red-cockaded Woodpeckers create and maintain a sap barrier around entrances to brood cavities, presumably to avoid predation by snakes (Rudolph et al. 1990). However, gray rat snakes (*Elaphe obsoleta spiloides*) remain important predators of Red-cockaded Woodpecker eggs and nestlings (Jackson 1978, Rudolph et al.

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1990). Since Red-cockaded Woodpeckers are an endangered species and continue to decline in most portions of their range, mesh snake traps have been used to prevent rat snakes from climbing cavity trees (Neal et al. 1993).

Bienville National Forest is 72,216 ha of predominantly loblolly pine (*Pinus taeda*) forest in south-central Mississippi. It has 104 active clusters comprising the largest population of Red-cockaded Woodpeckers in Mississippi. The Noxubee National Wildlife Refuge, Noxubee County, Mississippi occupies 19,376 ha and has approximately 35 active Red-cockaded Woodpecker clusters.

The 1.91 cm (3/4″) mesh snake traps installed at Bienville National Forest and Noxubee National Wildlife Refuge are placed approximately 1 m above the ground and are similar to designs used elsewhere (Neal et al. 1993). Here, we document the mortality of two Red-cockaded Woodpeckers caused by mesh snake traps on the Bienville National Forest and two others on the Noxubee National Wildlife Refuge.

On 20 April 1997, S. Samano observed a dead Red-cockaded Woodpecker ensnared in a mesh snake trap at Bienville National Forest, Scott County. This bird was caught in a mesh snake trap installed on the brood tree during the 1997 breeding season. The bird was an adult female based on plumage characters and time of year. Only the head and neck of the bird remained in the snake trap. Several contour and flight feathers were found on the ground underneath the trap, but the rest of the bird was not located. Since little decomposition had occurred in the head and neck area, we estimate the bird was caught within several weeks prior to discovery. The specimen was deposited in the ornithological collection in the Biological Sciences Department at Mississippi State University.

On 18 June 1997, D. Wood and M. Taquino discovered a fledged juvenile male Red-cockaded Woodpecker dead in a mesh snake trap on a woodpecker roost tree in the Bienville National Forest. The juvenile bird had been observed alive three days prior to its discovery in the trap. This observation and lack of decomposition suggest the bird was ensnared within two days of discovery. The specimen was deposited in the ornithological collection of the Mississippi Museum of Natural Science.

On 19 June 1997, at the Noxubee National Wildlife Refuge, J. Cole found a live, banded Red-cockaded Woodpecker underneath a mesh snake trap. The mesh snake trap was placed on the tree as part of an ongoing study of rat snake ecology. The fledgling was not caught in the mesh, but was directly below the netting. The bird was removed and placed above the netting, but continued to move back down into the mesh trap. After several attempts, the bird was successfully placed on a different tree and all snake traps in the cluster were removed. The fledgling was 25 days old at the time. Two juveniles from the same clutch had previously fledged successfully and did not become ensnared in the mesh snake trap. The tree on which the fledgling was found was within the cluster but did not have a cavity.

On 24 April 1997, J. Cole found two dead, banded Red-cockaded Woodpecker fledglings caught in a single mesh snake trap on a brood tree at Noxubee National Wildlife Refuge. The fledglings, one male and one female, were approximately 34–35 days old based on band records and partial decomposition. There were no other nestlings in the clutch. In addition to the Red-cockaded Woodpeckers found dead in mesh snake traps, a dead Yellow-bellied Sapsucker (*Sphyrapicus varius*) was caught in a mesh snake trap at Bienville National Forest in the winter of 1996 (D. Elsen, pers. comm.).

The positions of the adult female (Bienville National Forest) and three fledglings (Noxubee National Wildlife Refuge) indicate they entered the snake traps from the base of the trees. The position of the juvenile (Bienville National Forest) suggests that it either landed directly on the trap or became entangled while moving down the tree. Our data suggest that juvenile Red-cockaded Woodpeckers are more susceptible to entanglement because of their poor flight performance and foraging position on trees.

There may be several explanations for how these woodpeckers were caught in the traps. Red-cockaded Woodpeckers exhibit sexual segregation in foraging location on trees. Males forage high in the crown whereas females forage almost exclusively on the trunk more than 1 m from the ground (Ligon 1968). Although Red-cockaded Woodpeckers do not

typically forage at the height of mesh snake skirts, foraging has been recorded within 2 m of the ground (D. Wood, unpubl. data). Instances of drinking from the ground and foraging on fallen slash and slash piles are further examples of activity at low heights (Ligon 1970, Shaefer et al. 1991).

Mesh snake traps are highly successful at capturing rat snakes on Red-cockaded Woodpecker cavity trees (Neal et al. 1993; Richardson and Stockie 1995; D. Wood., unpubl. data). Although these studies indicate a high rate of climbing by rat snakes, we cannot positively assert either that rat snakes would have successfully entered the brood cavity and depredated the nest, or conversely, that the resin barrier would have prevented entrance to the cavity.

Mesh snake traps have led to four known mortalities of Red-cockaded Woodpeckers, one mortality of a Yellow-bellied Sapsucker, and one live capture of a Red-cockaded Woodpecker. In July 1997, the U.S. Fish and Wildlife Service ordered the removal of all mesh snake traps from RCW cavity trees. Instead of mesh skirts, we recommend an alternative, non-lethal method tested by Withgott and coworkers (1995).

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Unambiguous Evidence of Helping at the Nest in Bridled Titmice

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ABSTRACT.—Two instances of helping behavior in Bridled Titmice (*Baeolophus wollweberi*) were observed. In each case, one auxiliary bird assisted in feeding chicks at a nest. Both helpers were male; one a hatching year bird and the other an after hatching year bird. It was possible to quantify the feeding efforts of all three birds at one nest, but not at the other. The importance of our findings lies in the rarity of helping behavior in the titmouse family (Paridae). *Received 30 Sept. 1997, accepted 3 Aug. 1998.*

Animals helping to rear young that are not their own seem to be acting in a way that is detrimental to their personal fitness. The question of why natural selection has maintained cooperative breeding in animal populations has sparked lively debate and considerable research (e.g., Emlen 1982a, b; Brown 1987; Stacey and Ligon 1991; Koenig et al. 1992). Cooperative breeding subsumes a wide variety of social systems among diverse taxa (Brown 1987); it appears that the factors influencing cooperative systems are equally diverse. Discussion of the significance of helping will most likely continue as more is learned about the ecological and phylogenetic relationships of cooperative breeders. Documentation of helping in poorly known species is thus essential to the development of theory in this area.

Here we present observations of one completely banded and one partially banded nesting unit of Bridled Titmice (*Baeolophus wollweberi*). Helpers may occur with some frequency in this species, at least in some areas; 6 out of 10 nests observed over the course of three years in the Huachuca Mountains of Arizona appeared to have had helpers present, and four cases of helpers at the nest have been reported in Durango, Mexico (Nocedal and Ficken, in press). Previous observations of helping behavior in this species have been of limited duration in largely unbanded populations. Thus it has been impossible in most cases to identify helpers, even as to age or sex, or to quantify their contributions. Helping is rare within the tit family (Paridae). The Black Tit (*Parus niger*) of South Africa appears to breed cooperatively on a regular basis (Tarboten 1981) and helpers have been reported occasionally in the Tufted Titmice (*B. bicolor*; Brackbill 1970, Davis 1978, Tarbell 1983). Cooperative breeding within this family is particularly interesting because of the vast amount of information available on the group (Smith 1991 and references therein).

In June 1997 we color banded Bridled Titmice and made systematic behavior observations at seven active nests in two canyons in the Chiricahua Mountains, Cochise Co., Arizona. In 1998 we banded and observed titmice at 21 nests in the same study areas. Each year, one nest was tended by three birds. In 1997, the nest with three birds present was found on 5 June, and contained four young chicks. It was located in a natural cavity in a live oak tree. The first attending bird, an after hatching year (AHY) male, was banded on 8 June. The second, an AHY female, was banded on 16 June. The third bird was banded on 18 June; a hatching year (HY) bird, which was male (based on wing measurement; Gaulin and Christman, unpubl. data). The bird was determined to be an HY bird by lack of feather wear, pale mouth lining (Pyle et al. 1987), and indistinct facial pattern (pers. obs.). Research on a wide array of species with helpers suggests that the HY helper we banded was probably from a previous brood raised by the AHY birds trapped at the nest; however, this supposition remains to be tested for Bridled Titmice. Double brooding does occur occasion-

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ally in our study area. In 1997, adults were observed simultaneously feeding a fledgling and building a nest, and in 1998 a banded pair successfully raised two broods. The chicks were banded in the nest on 19 June. We began observations of the nest after the first two adult birds were banded (16 June), and continued until 24 June. During 16.5 hours of observations, we observed 103 feedings. Thirty-nine (38%) were by the adult male, 39 (38%) by the adult female, and 25 (24%) by the helper. We did not see the adults feeding the HY helper during our nest watches or at any other time. The observations were spread uniformly throughout the day. The nest may have successfully fledged one chick; however, the other three nestlings were lost to predation. The predation of the third nestling occurred during a nest watch; it was taken by a cliff chipmunk (*Eutamias dorsalis*). The chipmunk ran into the hole, grabbed the nestling, and exited rapidly. From the behavior of the chipmunk, it seems probable that it was responsible for taking the other two nestlings. The nest was examined immediately after the predation, and only one chick remained. Until this time, we had avoided looking into the nest after banding the chicks, so we do not know when the first two nestlings disappeared.

In June 1998 we discovered a second instance of helping. Two birds were separately trapped and banded as they exited the nest after feeding nestlings: an AHY female (based on wing measurements and brood patch) and an AHY male (based on wing measurements and song; Ficken, pers. comm.) on 11 and 14 June, respectively. The presence of a third bird was detected on 13 June, after the banding of the first bird, when two unbanded birds were simultaneously observed at the nest cavity carrying food. The final unbanded bird became extremely wary after the trapping of the second bird, and ceased feeding the nestlings. However, it remained near the nest until the chicks fledged, singing and giving alarm calls. It did not remain with the family flock after the chicks fledged. Despite being unable to catch the third bird, we were able to determine that the unbanded helper was male (by song), and that it was an AHY bird (based on facial pattern, tail feather wear, song development, and the absence of independent fledglings in the population at this date). Five chicks were successfully fledged from the nest.

Phylogeny appears to influence the incidence of cooperative breeding (Edwards and Naeem 1993). Why might Bridled Titmice have helpers at the nest when the behavior is generally rare within the family? Parids exhibit some of the demographic and behavioral characters typical of cooperative species (Brown 1974). Most tit species form stable flocks, hold group territories in the non-breeding season, and are highly sedentary; habitat saturation appears to be a constraint on breeding in certain populations (Ekman 1988). In some populations, there appears to be high enough winter mortality so that breeding opportunities open in the spring; in others, floating non-breeders appear to be common (Odum 1942, Weise and Meyer 1979). The similarity between the ecology of titmice and cooperative species has been discussed previously (Ekman 1989, Matthysen 1990).

Bridled Titmice differ from other parids in the timing of natal dispersal which may make helping behavior more likely to evolve. In most well studied tit species, the winter flocks form in the late summer with juveniles dispersing from their natal territories, finding mates, and joining an adult pair (or sometimes multiple pairs) on the adults' territory (Ekman 1989, Matthysen 1990). Juveniles that establish themselves on a territory earlier have a higher dominance rank which in turn leads to higher survivorship over the winter and a higher probability of breeding in the spring (Brawn and Samson 1983, Nilsson and Smith 1988). Early dispersal of juveniles to these winter flocks is therefore under strong selection and young birds leave the parental territory as early as 12 days post-fledging (Nilsson and Smith 1988). Early dispersal appears not to be of primary importance in Bridled Titmice, however. Juveniles remain on the parental territory for a minimum of 34 days and some stay for over six weeks (Christman, unpubl. data). In the case of the HY helper, the individual may not have suffered a fitness cost by remaining on the (presumed) parental territory, though the question of why it assisted in rearing the young remains unanswered. The presence of an AHY helper in 1998 indicates that there may be other reasons why individuals help. Until we have collected more data

on both the behavior and relatedness of helpers to the breeding pair it is not possible to speculate why mature individuals help at the nest in this species.

At present the importance of helping at the nest in Bridled Titmice lies in its relative taxonomic isolation. The fact that this behavior is rare among other members of the family makes this taxonomic group a fertile ground for comparative testing of theories of cooperative breeding.

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Swainson's Thrush Caught in Enchanter's Nightshade

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ABSTRACT.—On 10 September 1993, I was tending the banding nets for the Rouge River Bird Observatory (RRBO) at the University of Michigan–Dearborn, Wayne Co., Michigan. On my way down the net lanes, I noticed a bird struggling in the weeds. It was a Swainson's Thrush (*Catharus ustalatus*) thoroughly caught by the wings in the seed pods of a clump of enchanter's nightshade (*Circaea quadrisulcata* syn. *lutetiana*). Despite the bird flapping even more vigorously as I approached, it could not free itself. I disengaged the bird from the plant and returned to the banding lab. The bird was an apparently healthy hatching-year individual that weighed 32.1 grams. (The mean weight of 472 Swainson's Thrushes banded at

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RRBO is 32.7 g.) *Received 23 Aug. 1997, accepted 2 June 1998.*

There are numerous accounts of small birds being entangled in burdock (*Arctium minus*). They include four Ruby-throated Hummingbirds (*Archilochus colubris*), three Black-capped Chickadees (*Poecile atricapillus*), one Red-breasted Nuthatch (*Sitta canadensis*), well over a dozen Golden-crowned Kinglets (*Regulus satrapa*), two Ruby-crowned Kinglets (*Regulus calendula*), one each Blue-gray Gnatcatcher (*Polioptila caerulea*), Solitary Vireo (*Vireo solitarus*), Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler (*Dendroica coronata*), Common Yellowthroat (*Geothlypis trichas*) and Pine Siskin (*Cardulis pinus*), two unidentified warblers, and several American Goldfinch (*Carduelis tristis*) (McNicholl 1988, 1994; Wright 1984). Hampson (1970) provides the only report of birds trapped in a plant other than burdock: a House Wren (*Troglodytes aedon*) and a Ruby-crowned Kinglet entangled in beggar's lice (*Hacklelia virginiana*).

The seed heads of burdock are fairly large (1.5–3 cm), and the plant itself is robust. The fruits of beggar's lice are also bur-like, approximately 8 mm wide. With the exception of the Solitary Vireo, all of the victims are small birds; for example, the mean weight of Golden-crowned Kinglets (the most frequent victims) is just over 6 g (Dunning 1993). In contrast, enchanter's nightshade is a relatively weak plant, with very small (<3 mm) nut-like seeds covered with minute barbed hairs, giving a Velco®-like effect. This is the first reported instance of a bird being caught in enchanter's nightshade, and the Swainson's Thrush is the largest bird reported entangled in seed heads.

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Comparisons of Wintering Bird Communities in Mature Pine Stands Managed by Prescribed Burning

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ABSTRACT.—We compared the effects of growing season and dormant season prescribed fire on the winter bird communities in mature pine stands on Fort Benning Military Reservation, Georgia. We surveyed the avian community using fixed-radius point counts from 1 December 1995 to 28 February 1996, one year after burning. We detected no differences in mean bird abundance or species richness between burn treatments. No species was observed more or less frequently in either burn treatment. Season of burn had little apparent effect on the composition of wintering bird communities in managed mature pine forests. *Received 31 March 1998, accepted 30 July 1998.*

Winter mortality may be a limiting factor for many resident birds in North America (Arcese et al. 1992), and the alteration or loss of winter habitats could contribute to avian population declines (Terborgh 1989, Morton 1992). Consequently, conditions on the wintering ground can influence breeding populations in following years (Baillie and Peach 1992) through competition for winter habitats

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TABLE 1. Vegetation characteristics, expressed as $\bar{x}$ (± SE), for growing and dormant season prescription burned mature pine stands on Fort Benning Military Reservation, Georgia (July–August 1995).

Habitat characteristic	Growing (n = 9)	Dormant (n = 9)	F-Value	P-Value
Stand age (years)	51.6 (4.3)	57.7 (4.0)	0.22	>0.05
Basal area (m^2/ha)	11.8 (1.4)	13.9 (1.8)	0.54	>0.05
Canopy closure (%)	31.7 (0.9)	31.0 (0.8)	0.12	>0.05
Shrub density (no./0.04 ha)	10.2 (0.8)	8.2 (0.8)	0.62	>0.05

(Holmes et al.1989, Rappole et al. 1989) and effects on winter site fidelity (Kricher and Davis 1986, Sherry and Holmes 1992). Therefore, it is important to understand how land management activities may affect avian use of winter habitats.

In the southeastern United States, prescribed burning is a widely used silvicultural tool in the management of pine forests. Historically, lightning caused fires have been a major ecological force in southeastern ecosystems (Komarek 1962, Landers 1987). Such fires usually occurred during the growing season (Komarek 1968, Taylor 1969), but during this century forest managers have relied predominately upon prescribed fires during the dormant season to manage forest understories. Burns conducted during the winter months provide conditions such as high moisture content of the vegetation, low ambient temperatures, and consistent winds, that reduce the chances of wildfire. Recently, growing season burns are being used more frequently by forest managers because they more closely mimic natural fire regimes and provide greater control of hardwoods. Although some researchers report favorable responses of breeding bird communities to burned versus unburned habitats (Emlen 1970, Wilson et al. 1995), research on the effects of prescribed fire on wintering bird communities is limited (Blake 1982). Because the season of burn can influence the vegetational structure of a habitat (Waldrop et al. 1992), we deemed it important to compare wintering avian communities in growing season and dormant season prescription-burned mature pine stands.

STUDY AREA AND METHODS

Our study was conducted at the Fort Benning Military Reservation near Columbus, Georgia. Fort Benning is located in the Upper Coastal Plain of west-central Georgia. The vegetation on Fort Benning is dominated by pure and mixed stands of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and shortleaf pine (*P. echinata*) with open understories consisting mainly of sweetgum (*Liquidambar styraciflua*), flowering dogwood (*Cornus florida*), andropogon (*Andropogon* spp.), blackberry (*Rubus* spp.), gallberry (*Ilex* spp.), and wax myrtle (*Myrica cerifera*). Pine stands on the reservation are managed with both growing season and dormant season prescribed fires on 3-year rotations. Many of the stands are managed to provide required habitat conditions for the Red-cockaded Woodpecker (*Picoides borealis*), an endangered species endemic to mature pine forests in the southeastern United States (U.S. Fish and Wildlife Service 1985). These stands are burned by prescription every 2–4 years.

We selected for study 9 plots that were burned in the growing season (April–August) and 9 plots that were burned in the dormant season (January–March) of 1994. All plots were located in mature pine stands within managed Red-cockaded Woodpecker habitat and were similar in basal area, canopy closure, and shrub density (Table 1). Because our interest was in comparing the avifauna of growing season burned areas to dormant season burned areas, we did not sample unburned plots. When comparing conditions in fire-maintained habitats, fire exclusion usually is considered a treatment rather than a control (Platt et al. 1988).

We censused birds in each plot along a line transect consisting of 9 census points located at least 122 m apart within managed, mature pine stands. Transect points were placed in 3 × 3 grids and were located at least 100 m from roads and other open areas (White et al. 1996). We conducted biweekly counts from mid-December 1995 through mid-February 1996, using the fixed-radius point count method (Hutto et al. 1986). Census methods were derived from Ralph and coworkers (1995). To reduce bias, plots were censused at alternate times between sunrise and 10:30 EST (Robbins 1981, Blake et al. 1991) and were alternated between observers (Erwin 1982). During each count, observers sampled each survey point for 5 minutes and all birds detected aurally or visually within a 61 m radius were counted. Flagging tape streamers were placed 15 m, 30 m, 45 m, and 61 m in the four cardinal directions from each point to assist observers in estimating bird distances. Birds flushed when observers were approaching or leaving a survey point were recorded, but birds flying over the plot were not included in the data analysis. Because all plots were relatively

TABLE 2. Mean (SE) nonbreeding bird abundance (mean no./per plot) on growing and dormant season prescription burned mature pine stands at Fort Benning Military Reservation, Georgia, December 1995 through February 1996.

Avian species	Growing	Dormant	*t*	*P*-Value
American Crow (*Corvus brachyrhynchos*)	0.14 (0.08)	0.29 (0.16)	0.68	0.42
American Goldfinch (*Carduelis tristis*)	0.13 (0.09)		2.23	0.16
American Kestrel (*Falco sparverius*)		0.02 (0.02)	1.00	0.33
American Robin (*Turdus migratorius*)	4.85 (2.27)	8.10 (3.63)	0.57	0.46
Bachman's Sparrow (*Aimophila aestivalis*)		0.14 (0.10)	2.14	0.16
Black Vulture (*Coragyps atratus*)		0.02 (0.02)	1.00	0.33
Blue Jay (*Cyanocitta cristata*)	0.13 (0.07)	0.09 (0.05)	0.21	0.65
Brown-headed Nuthatch (*Sitta pusilla*)	1.36 (0.36)	0.90 (0.22)	1.18	0.29
Carolina Chickadee (*Poecile carolinensis*)	1.44 (0.29)	1.75 (0.35)	0.48	0.50
Carolina Wren (*Thryothorus ludovicianus*)	2.10 (0.36)	1.80 (0.35)	0.39	0.54
Cedar Waxwing (*Bombycilla cedrorum*)	1.40 (0.87)	1.24 (0.68)	0.02	0.89
Chipping Sparrow (*Spizella passerina*)	0.59 (0.23)	0.20 (0.09)	2.55	0.13
Common Grackle (*Quiscalus quiscula*)	0.09 (0.09)		1.00	0.33
Common Snipe (*Gallinago gallinago*)		0.02 (0.02)	1.00	0.33
Common Yellowthroat (*Geothlypis trichas*)	0.06 (0.05)	0.07 (0.06)	0.02	0.88
Dark-eyed Junco (*Junco hyemalis*)	2.15 (1.50)	0.72 (0.19)	0.90	0.36
Downy Woodpecker (*Picoides pubescens*)	0.53 (0.15)	0.80 (0.13)	1.81	0.20
Eastern Bluebird (*Sialia sialis*)	1.48 (0.66)	0.68 (0.25)	1.31	0.27
Eastern Phoebe (*Sayornis phoebe*)	0.56 (0.18)	0.44 (0.19)	0.22	0.64
Eastern Towhee (*Pipilo erythrophthalmus*)	1.54 (0.33)	2.31 (0.68)	1.04	0.32
Eastern Wood-Pewee (*Contopus virens*)		0.02 (0.02)	1.00	0.33
Fox Sparrow (*Passerella iliaca*)	0.04 (0.04)		1.00	0.33
Gray Catbird (*Dumetella carolinensis*)	0.04 (0.04)		2.29	0.15
Golden-crowned Kinglet (*Regulus satrapa*)	0.07 (0.07)	0.47 (0.33)	1.37	0.26
Hairy Woodpecker (*Picoides villosus*)		0.10 (0.05)	3.61	0.08
Hermit Thrush (*Catharus guttatus*)	0.36 (0.16)	0.54 (0.18)	0.57	0.46
Mourning Dove (*Zenaida macroura*)	0.06 (0.04)	0.07 (0.05)	0.01	0.91
Northern Cardinal (*Cardinalis cardinalis*)	1.13 (0.21)	0.91 (0.19)	0.55	0.47
Northern Flicker (*Colaptes auratus*)	0.27 (0.08)	0.24 (0.09)	0.08	0.78
Palm Warbler (*Dendroica palmarum*)	0.02 (0.02)		1.00	0.33
Pileated Woodpecker (*Dryocopus pileatus*)	0.30 (0.16)	0.10 (0.05)	1.32	0.27
Pine Warbler (*Dendroica pinus*)	3.32 (1.26)	4.55 (2.31)	0.22	0.65
Prairie Warbler (*Dendroica discolor*)	0.34 (0.20)	0.07 (0.07)	1.48	0.24
Red-bellied Woodpecker (*Melanerpes carolinus*)	1.18 (0.19)	0.87 (0.27)	0.90	0.36
Red-breasted Nuthatch (*Sitta canadensis*)	0.04 (0.04)	0.02 (0.02)	0.12	0.74
Red-cockaded Woodpecker (*Picoides borealis*)	1.57 (0.53)	0.90 (0.48)	0.89	0.36
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	0.07 (0.07)	0.16 (0.10)	0.41	0.53
Red-shouldered Hawk (*Buteo lineatus*)	0.02 (0.02)	0.02 (0.02)	0.02	0.90
Ruby-crowned Kinglet (*Regulus calendula*)	0.62 (0.23)	1.12 (0.40)	1.20	0.29
Song Sparrow (*Melospiza melodia*)	0.06 (0.04)		2.00	0.18
Solitary Vireo (*Vireo solitarius*)	0.08 (0.08)	0.04 (0.04)	0.15	0.71
Tufted Titmouse (*Baeolophus bicolor*)	0.65 (0.22)	0.99 (0.42)	0.50	0.49
Turkey Vulture (*Cathartes aura*)		0.04 (0.04)	1.00	0.33
White-breasted Nuthatch (*Sitta carolinensis*)	0.59 (0.20)	0.17 (0.09)	3.54	0.08
White-throated Sparrow (*Zonotrichia albicollis*)	0.78 (0.28)	1.81 (0.77)	1.61	0.22
Wild Turkey (*Meleagris gallopavo*)	0.19 (0.19)		1.00	0.33
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	0.45 (0.15)	0.21 (0.07)	2.07	0.17
Yellow-rumped Warbler (*Dendroica coronata*)	0.46 (0.18)	0.33 (0.10)	0.36	0.56

open, the probability of detecting birds was assumed to be equal (Dawson 1981, Verner and Ritter 1986). Counts were not conducted on days with moderate rain or wind.

Avian species were grouped by habitat preference into four categories: forest interior species, interior-edge species, edge-field species, and field species (Whitcomb et al. 1981, Freemark and Collins 1992). Since the census points in each plot were not independant, we considered the sum of birds observed during

TABLE 3. Mean (SE) avian abundance and richness in growing and dormant season prescription-burned mature pine stands at Fort Benning Military Reservation, Georgia, December 1995–February 1996.

Habitat preference	Abundance (no./plot)			Richness (S)		
	Growing	Dormant	*F*-value	Growing	Dormant	*F*-Value
Forest interior species	5.9 (1.4)	4.0 (0.7)	1.55	5.1 (0.5)	4.3 (0.3)	1.62
Interior-edge species	12.9 (1.1)	12.6 (1.1)	0.04	4.0 (0.3)	4.4 (0.2)	1.39
Edge-field species	6.2 (2.0)	5.1 (1.4)	0.20	4.6 (0.3)	3.9 (0.4)	2.12
Field species	7.6 (2.0)	5.4 (1.3)	0.85	13.2 (0.5)	12.8 (0.7)	0.24
Total	30.2 (3.9)	23.2 (2.5)	2.29	26.9 (0.9)	25.4 (0.7)	1.65

the censuses of the 9 points as one count. Annual means for bird abundance, richness, and diversity were derived from census totals ($n = 6$) for each plot. Differences between treatments were tested (SAS Institute, Inc. 1990) using a one-way analysis of variance (ANOVA). Bird species diversity was determined for each plot in each burn treatment using the Shannon-Weiner Index (Shannon and Weaver 1949). Data for individual species were transformed by adding 0.5 and calculating the square-root of all values (Steel and Torrie 1960). Differences in individual bird species abundance between burn treatments were analyzed (SAS Institute, Inc. 1990) using a *t*-test. Null hypotheses for all tests were rejected at $P \leq 0.05$.

RESULTS AND DISCUSSION

To our knowledge, no researchers have reported on the effects of season of burn on nonbreeding bird communities in mature upland pine stands. We detected a total of 48 avian species, but we found only 41 species in the plots for each burn season. Fourteen species were observed only in growing season plots and 14 species were observed only in dormant season plots. The number and composition of avian species that we observed (Table 2) is consistent with those found wintering in mature pines of the Piedmont physiographic region of Georgia (White et al. 1996). No species was observed ($P > 0.05$) more in either burn treatment. Avian communities did not differ ($P > 0.05$) in mean abundance or richness between growing and dormant-season burned habitats (Table 3).

Season of burning in mature upland pines apparently has no significant effect on the wintering bird communities. The detection of flocking birds often is reduced during winter (Yahner 1985), and this could have resulted in fewer observations and undetected species using the different burn regimes.

Avian community parameters were higher ($P < 0.05$) in mature pine stands managed with prescribed fire than in 20–30 year-old unburned pine plantations in the central Georgia Piedmont (White et al. 1996). Mature pines provided habitat conditions favorable to the Red-cockaded Woodpecker and also created habitat conditions suitable for many wintering avian species.

Although characteristics of the wintering bird communities did not differ between burn treatments, our study was limited to the nonbreeding season and did not compare the effects season of burn may have on breeding bird communities. Long-term studies comparing the effects season of burn in pine stands have on wintering and breeding bird communities are needed. With the limited research describing the effects season of prescribed burning has on avian communities, we suggest that land managers use both growing and dormant season prescribed fires to create a mosaic of habitat types.

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Egg Size and Cotton Rat Predation

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ABSTRACT.—Although cotton rat (*Sigmodon hispidus*) presence at predated Northern Bobwhite (*Colinus virginianus*) nests has been widely reported, it is unclear how often cotton rats are the actual predators. We presented two sizes of eggs to 35 wild-trapped cotton rats to better understand how avian egg size affects nest predation in the wild. Zebra Finch (*Poephila guttata*) eggs (16.0 × 11.4 mm) and Northern Bobwhite eggs (30.0 × 24.7 mm) were presented to captive cotton rats in 30 × 30 cm enclosures. Eggs were checked every 6 h for 24 h. Food was withheld from 18 of the rats in an attempt to induce egg consumption. No cotton rats consumed bobwhite eggs (0/35 cotton rats), but Zebra Finch eggs were frequently consumed (29/35 cotton rats). The gapes of cotton rats used in this study were smaller than the bobwhite egg widths and may have prevented cotton rats from successfully cracking the eggshells. It is apparent that cotton rats will readily consume eggs smaller than those of the Northern Bobwhite and pose a predation threat to passerines. Based on our data and known abundances of cotton rats throughout their range, we conclude that cotton rats pose a significant threat to smaller birds nesting on or near the ground. However, we offer no evidence to implicate cotton rats as important predators of bobwhite nests. *Received 28 Aug. 1997, accepted 30 July 1998.*

Cotton rats (*Sigmodon hispidus*) are one of the most abundant small mammals of open habitats of the southeastern United States with densities of 24–30 per ha in some areas (Schwartz and Schwartz 1981). These same habitats provide nesting grounds for Northern Bobwhite (*Colinus virginianus*) and several songbird species for whom population declines have been reported (Sauer et al. 1996). Cotton rats have been reported as important predators of Northern Bobwhite nests (e.g., Stoddard 1931, Simpson 1976, Hawthorne 1983). However, supporting evidence is mostly circumstantial. Stoddard (1931) mentioned the use of captive cotton rats in egg presentation experiments but failed to report his results.

Artificial nests have been widely employed to compare predation rates among different habitats and habitat patch sizes (e.g., Wilcove 1985; Burger et al. 1994; Leimgruber et al. 1994). Most artificial nest studies have used Japanese Quail (*Coturnix japonica*) or Northern Bobwhite eggs, which are much larger than the eggs of most passerines. Small-mouthed predators may be unable to consume the larger eggs while being entirely capable of eating smaller eggs (Reitsma et al. 1990; Roper 1992; Haskell 1996a, b). An artificial nest study using bobwhite eggs conducted in western Tennessee in summers 1996 and 1997 documented that cotton rats were frequently responsible for nest and egg disturbance. However, these disturbances rarely resulted in actual damage to the bobwhite eggs (Ettel, unpubl. data).

The objective of this study was to determine the effect of egg size on egg comsumption and to test the hypothesis that cotton rats are often prevented from predating bobwhite eggs because they are unable to bite into them.

METHODS

Thirty-five wild cotton rats (21 females, 12 males, and 2 animals of unknown sex) were collected on the Ames Plantation in Fayette County, Tennessee, in December 1996 and January 1997 using Sherman live traps baited with a mixture of rolled oats and peanut butter. Rats were weighed, sexed and placed into wire cages (30 × 30 cm) in a vacant, unheated building and acclimated for at least 12 hours. Cages were lined with straw for bedding. Because of a lack of available space, 4 cotton rats were placed in larger holding cages. Daily temperatures ranged from −2.2 to 2.7° C and nightly temperatures ranged between −16.1 and −0.6° C between 19 December 1996 and 12 January 1997, when the experiment was conducted.

To induce consumption of the eggs, food was withheld from one group of cotton rats to create an emaciated state. Eighteen of the 35 cotton rats were initially given food consisting of peanut butter and water.

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Food was withheld from the other 17 immediately before and during egg presentation, a duration of 36–48 hours. Unfed rats were weighed both before and after the experiment to check for weight loss. χ^2 analysis was used to test for differences in egg consumption between fed and unfed groups.

Cotton rats were presented with two 11-cm diameter grass nests, one containing a Zebra Finch (*Poephila guttata*) egg and clay mimic and the other a Northern Bobwhite egg and clay mimic. Clay eggs were made of Plastalina®, a soft, malleable modeling clay. Clay eggs were used to simulate conditions of the artificial nest study we conducted in 1996 and 1997 in which both artificial eggs and real eggs were used (Ettel, unpubl. data). Nests were left in the cages for 24 h and egg fate was recorded every 6 h. At the conclusion of the experiment, all cotton rats were euthanized and gape measurements were taken. We used *t*-tests to determine differences in gape or weight according to sex.

Shell thickness of 20 bobwhite eggs from the same commercial game farm as those used in the experiment and 20 bobwhite egg shells from hatched nests of wild birds collected from Fayette and Houston counties, Tennessee was measured using digital calipers. A *t*-test was used to test for differences in shell thickness between the two groups.

We used a logistic regression model to test the effects of the measured variables on both the fate (consumed or not consumed) of each individual egg and the time interval (6 h, 12 h, 18 h, 24 h) in which an egg was consumed (Agresti 1990). Explanatory variables used in the model were: weight, gape, sex (male or female), egg type (clay or real), and egg size (bobwhite or finch) as well as all possible interaction terms. Gape and weight were both treated as continuous variables whereas all other variables represented discrete, binary variables. The stepwise selection procedure was employed to fit a model from the available explanatory variables. A likelihood ratio test and its associated χ^2 statistic was utilized to test model suitability, with significance level set at $P < 0.05$. Individual variables within the final model were tested for significance using the Wald statistic and its associated χ^2, with a significance level set at $P < 0.05$ (Agresti 1990). Analyses were conducted using PROC LOGISTIC from SAS statistical software, version 6.12, on a personal computer (SAS Inst., Inc. 1997).

The four cotton rats held in larger holding cages were not used in these analyses to eliminate potential bias associated with cage size.

RESULTS

Twenty-eight of 35 cotton rats (80%) ate finch eggs but none ate bobwhite eggs. Clay eggs were commonly bitten and partially consumed (31/35 of finch-sized and 23/35 of bobwhite-sized eggs). Some contact with bobwhite eggs by cotton rats was apparent as eggs were often found removed from the nests to other parts of the cages, sometimes buried underneath the straw bedding or the nest itself.

There was no difference in finch egg consumption between fed and unfed cotton rats ($\chi^2 = 0.019$, df = 1, $P > 0.05$), therefore we pooled data from the two groups for the analysis. Mean weight for 33 rats (we were unable to attain weights for 2 rats) was 75.8 ± 30.5 g with no differences between sexes ($t = -0.623$, df = 31, $P > 0.05$). Mean gape size for 31 rats (we were unable to measure gape on 4 rats) was 13.7 ± 2.4 mm with a range of 9.8–18.9 mm and no difference between sexes [$t = -0.030$, df = 25.9 (unequal variances), $P > 0.05$].

Bobwhite eggs averaged 30 × 24.7 mm, whereas finch eggs averaged 16 × 11.4 mm. Thus, bobwhite eggs were 5.8–14.9 mm wider than cotton rat gapes reported in this study, whereas finch egg widths fell within the range of cotton rat gapes. No difference in thickness was found between the wild and domestic bobwhite eggshells ($t = 1.38$, df = 25.9 (unequal variances), $P > 0.05$).

The stepwise selection procedure eliminated all interaction terms and the variables sex and gape in creating a model for egg fate. A final model for egg fate with the variables weight, type, and size was fit (log likelihood, df = 3, $P < 0.001$). The variables weight ($\beta = -0.0321$, Wald $\chi^2 = 6.2949$, $P = 0.012$), type ($\beta = -2.9696$, Wald $\chi^2 = 17.2113$, $P < 0.001$), and size ($\beta = 3.5079$, Wald $\chi^2 = 22.8898$, $P < 0.001$) were individually significant within the model. Negative parameter estimates for both type and weight indicate that clay eggs were more likely to be consumed than real eggs, partially resulting from clay bobwhite eggs frequently being eaten whereas real bobwhite eggs never were. Heavier rats were also more likely to consume eggs than lighter individuals. Parameter estimates for egg size indicate that finch eggs were more likely to be consumed than bobwhite eggs.

For the elapsed time of egg consumption, stepwise selection did not identify any of the explanatory variables as important ($P > 0.05$). This result was apparently caused by egg consumption occurring within the initial 12 hours.

The 17 unfed animals experienced an average weight loss of 7.4 ± 6.0g (9.8 % average decrease in weight). This may represent a

significant weight loss. A change in weight was not documented for the 18 rats that were provided food.

After our observation that no cotton rats consumed or even damaged the bobwhite eggs, we presented the 4 remaining cotton rats with broken bobwhite eggs. All four rats ate the damaged eggs including all egg contents and large portions or all of the shell. When subsequently presented a second unbroken bobwhite egg, none of these four rats consumed the egg. The range of gape sizes for these four rats was 11.5–17.5 mm, and thus was similar to the gape sizes of our entire sample.

DISCUSSION

Although cotton rats are widely reported as bobwhite nest predators, our results document the ability of cotton rats to consume small passerine-sized eggs but not bobwhite eggs. Stoddard (1931) and Simpson (1976) present two of the only studies that attribute bobwhite nest predation to cotton rats based upon actual field sign (hair and feces around the nest and egg shell fragments in cotton rat runways). However, Leimgruber and coworkers (1994) noted that several predators often visit a single nest. With the use of motion-sensitive cameras, Fenske-Crawford and Niemi (1997) recorded several small rodents visiting nests without damaging eggs. We suspect that cotton rat presence at predated nests can be accounted for in two ways. Upon finding a nest that has been predated previously by another animal, cotton rats may consume damaged eggs or egg shells at the nest or carry some away. Additionally, as noted in our artificial nest study (Ettel, unpubl. data), cotton rats often destroy the nest itself, scatter eggs, and sometimes carry eggs a short distance away from the nest, all without damaging eggs. These actions could make nests more visible to other predators, thereby making cotton rats accessories to predation, but not actually egg predators themselves.

In this study, although rats moved bobwhite eggs to different parts of the cages, they failed to consume any undamaged bobwhite eggs. However, the smaller finch eggs were frequently eaten. Cotton rats consumed cracked and broken bobwhite eggs presented to them, indicating that the eggs were both palatable to them and that the season of the year and cold temperatures had no effect upon their consumption of eggs.

We believe that the substantial weight loss documented in cotton rats over the short period of the feeding trial demonstrated emaciation. Haskell (1996a) suggested that inexperienced animals may not know how to eat quail eggs, but our cotton rats were taken from an environment in which bobwhite are common. After consuming a broken bobwhite egg, four cotton rats in our study failed to damage an unbroken bobwhite egg when presented with one. Because the commercial bobwhite egg shells used were similar in thickness to egg shells of wild birds, if these cotton rats were capable of eating bobwhite eggs in the wild, then they should have been capable of eating the eggs in this experiment.

After measuring gapes of some small rodents, DeGraaf and Maier (1996) and Haskell (1996a) concluded that some small rodents are unable to bite into quail eggs. Our gape measurements suggested that cotton rats used in this experiment had gapes that were too small to bite into a bobwhite egg. Bobwhite egg widths were larger than the measured gapes. In the wild, predation of bobwhite eggs may require extraordinary effort and may occur only under unique conditions, such as when alternative foods are scarce. Both Stoddard (1931) and Simpson (1976) reported an increase in cotton rat predation of bobwhite nests when cotton rat densities were abnormally high. Additionally, cotton rats do reach weights greater than the largest rat used in this study (165 g; Schwartz and Schwartz 1981). The failure of the rats in this study to eat undamaged bobwhite eggs may indicate that most cotton rats have gape sizes too small to penetrate the eggshell and that only the largest cotton rats may be able to efficiently handle bobwhite eggs.

Our results suggest that cotton rat predation on songbird nests placed on the ground or in vegetation near ground level could be significant. Additionally, by disturbing active nests, cotton rats may possibly be accessories to predation or may induce abandonment of nests by bobwhite hens. However, because of the inability of cotton rats to damage bobwhite eggs in this study, we can offer no evidence to implicate cotton rats as important predators

of bobwhite eggs. We suggest that further study be conducted to determine the effect cotton rats have on breeding songbirds in agricultural areas throughout their range, focusing upon evidence beyond the circumstantial. Additional work is needed to quantify claims of significant bobwhite nest predation by cotton rats.

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Ornithological Literature

Edited by William E. Davis, Jr.

AVIAN MOLECULAR EVOLUTION AND SYSTEMATICS. D. P. Mindell, Ed. Academic Press, San Diego, California 1997: 382 pp. $69.95.—Have you ever wondered where the Wancy region is? Or thought about avian numts or the putatively primative Pelecaniforms? There has been a not so quiet revolution going on—building like a logistic growth curve since before the days of Charles Sibley's studies of egg white protein as an indicator of systematic relationships—one with a vocabulary that many ornithologists don't recognize. Now it is exploding into the popular press and onto movie screens through blockbusters such as Jurassic Park. The revolution is not just in our understanding of the inherited chemistry of life. It is also in the way we "do" life. The revolution is having an increasing influence on fields as diverse as ecology, behavior, systematics, conservation, and, yes, even the entertainment industry and our judicial system.

This revolution has been made possible by the development of increasingly sophisticated procedures, by those holding purse strings who have seen the potential for these studies, but mostly by dreamers: scholars who have had the brilliance to ask questions beyond the realm of "conventional biology," dared to invest their careers in seeking answers to those questions, and had the stature and supreme self-confidence to present and defend their work to the scientific community and the world. Yes, along with such progress comes an imaginative vocabulary too.

Avian Molecular Evolution and Systematics is both a primer for those excited or curious about this revolution and a status report of the rapidly growing field. The insights promised by study of egg white proteins and DNA-DNA hybridization were a mere trickle when compared to the potentials of new studies involving the mitochondrial genome. This book is also a reality check and a reassurance for students of morphological variation. High hopes for unlocking a simple key to all evolutionary and systematic answers have been dashed by the realization that, as editor Mindell says, "the evolution of some molecular characters can be as quirky and unique to individual lineages as that seen for some phenotypic characters."

I congratulate the editor on the organization and presentation of this book—it is quite user-friendly in spite of the sometimes complex and esoteric subjects. The one addition that would have made it even more user friendly would have been a glossary that included some of the esoteric terms of molecular systematics. The index helps, since some terms used in earlier chapters are better defined in later ones. The 13 chapters include the efforts of 32 authors and are divided into two major sections: Molecular Sequences and Evolutionary History in Birds (8 chapters), and Applying Phylogeny and Population Genetics to Broader Issues (5 chapters). Authors represent major museums and universities from the United States, Canada, Great Britain, and Denmark. The list of Contents includes not only chapter titles and authors, but also an outline of each chapter indicating the beginning page for each chapter subheading. In a bit of generous redundancy, these outlines are repeated on the first page of each chapter, thus facilitating use for those who rely on reprints rather than buy the book.

Chapters vary from those that focus on techniques, their variations, possibilities, and limits (Chapters 1–4, 9), to application of those techniques to the systematics of Gruiformes (Chapter 5), Pelecaniformes (Chapter 6), and ratites (Chapter 7), to the use of the techniques in ecology (Chapter 10), studies of geographic variation (Chapter 11), speciation (Chapter 12), and studies of paleoecology and conservation (Chapter 13).

Most of the chapters identify pitfalls and provide guidance for practitioners. But different molecular approaches, like using different suites of morphological characters, can provide different answers to the same question. Often such differences can be attributed to differences in interpretation. As a result, contro-

versy abounds even within the molecular systematist community. Relationships among the ratites provide a case in point in this volume: Krista Lee and coworkers (Chapter 7) place kiwis as a basal group and link them with moas, whereas Alan Cooper (Chapter 13) places kiwis in a derived position distant from the moas. One thing seems certain to me: far too much use is made of the word "indicates" in this book and in much of current ornithology. Authors should take a good hard look at the solidity of their data relative to the solidity of their opinion—"suggests" is such a fine word and is usually a much more appropriate alternative.

Certainly this is a book that belongs in university libraries and on the shelves of those with interests in molecular systematics and the application of molecular techniques to other biological endeavors. Michael Crichton might even find some useful material here!—JEROME A. JACKSON.

MONITORING BIRD POPULATIONS: THE CANADIAN EXPERIENCE. Erica H. Dunn, Michael D. Cadman and J. Bruce Falls, Eds. Occasional Paper Number 95, Canadian Wildlife Service: 62 pp., 12 figs., 16 tables. For information about this publication contact: Publications, Canadian Wildlife Service, Environment Canada, Ottawa, Ontario KIA 0H3 (E-mail: mark.hickson@ec.gc.ca).—This is a collection of nine articles from a proceedings of a symposium sponsored by the Society of Canadian Ornithologists and the Wilson Ornithological Society, held in conjunction with the joint meeting of these two societies in Guelph, Ontario, on 29 April–2 May 1993. The objective of the symposium was to provide an up-to-date summary of the kinds of monitoring programs currently underway in Canada. The editors and 15 authors fulfill this objective by producing nine information-rich chapters that cover the major, broad-scale multispecies monitoring programs in Canada aimed at tracking changes in species abundance. The papers are short (generally less than 6 pages each), concise, and well supported with tables and figures. The first few papers deal with waterfowl, seabirds, and shorebirds, which are monitored by government agencies. The remaining six papers deal mainly with land birds, where most of the methods rely on participation of volunteers. The collection of papers documents an impressive effort that is underway in Canada to monitor bird populations. The authors repeatedly point out research gaps either to identify areas of needed study or to suggest caution regarding interpretation. Two of the results that I found most intriguing were the significant relationships between results of the Breeding Bird Survey and Migration Indices (Fig. 2, page 46) and between the Breeding Bird Survey and Christmas Bird Counts (Fig. 2, page 51). If trends for a particular species are similar among these independent monitoring programs, it gives additional confidence in the assessment of their status. For the uninformed or moderately informed, the publication also serves as a very useful starting point for references into various types of avian monitoring programs. For anyone interested in monitoring birds, I would recommend this publication.—THOMAS W. CUSTER.

THE BOOK OF INDIAN BIRDS: TWELFTH REVISED AND ENLARGED CENTENARY EDITION. By Sálim Ali, illus. by Carl D'Silva. Bombay Natural History Society and Oxford University Press, Mumbai (Bombay). 1996: 354 pp., 64 color plates. Rs. 450 (cloth).—This book was issued to celebrate the centennial of the birth of the late Sálim Ali, India's most prolific, incisive, and uncompromising ornithologist. Having witnessed, first hand, Sálim Ali at work in the field, it was clear to me that his love for birds was as strong and as natural in his ninth decade as it was when he published the first edition of this book in 1941, six years before Indian Independence.

The name of Ali has long been associated with that of S. Dillon Ripley because of their ten-volume *Handbook of the Birds of India and Pakistan.* Ali's and Ripley's ornithological writings have become something of a cottage industry, not in the least deterred by the death of Ali and the retirement of Ripley. And this book continues (admirably) in that tradition. Featuring a wide selection of the birds found in India, this handy fieldbook would, I

believe, meet the approval even of Sálim Ali. The key to any field book is the collection of comparative plates, and this edition, with all new illustrations, provides an excellent, if incomplete, visual compendium of the subcontinent's birdlife. These plates are, overall, superior to those of the earlier editions as well as to those found in Ali and Ripley's *Pictorial Guide,* which currently stands as the fieldbook of choice for world birders visiting the region. I should note that the Indian "bird book landscape" will change drastically in the not-too-distant future with the expected publication of not one but two new field guides to the Indian Subcontinent (one British authorship, one American).

Until that time we must make do with what we have—which really is not so bad at all. I have used the *Pictorial Guide* in the field on a number of occasions and found it very useful, although flawed. The new Ali fieldbook looks to be a credible contender for the legion of eager local birders who wish to learn the birdlife without demanding to know all of the rarer species. There are useful facing page notes to the plates, and there are also functional species accounts in the main body of the text. This makes it a useful and user-friendly book for the majority of naturalists and bird-watchers in the region.

One problem facing the book is its linkage to a somewhat archaic nomenclature—that of Ripley's *Synopsis of the Birds of India and Pakistan,* now functionally superseded by the Oriental Bird Club's *Annotated Checklist of the Birds of the Oriental Region.* It will be interesting to see how the upcoming field guides handle the nomenclatural tangle produced by both higher level revisions following the Sibley and Ahlquist revolution and the availability of a series of English name options offered by the various regional and world checklists on the market today. In fairness to the Ali book, alternative names are included at the head of each species account.

This is a likable book that has been lovingly updated. It will find its largest market in India. That is only fitting, given Sálim Ali's strong nationalism, his unshakable love of Indian ornithology, and his multifaceted service to his nation as an ornithologist, conservationist, and senior government advisor.—BRUCE M. BEEHLER.

COLONIALITY IN THE CLIFF SWALLOW. C. R. Brown and M. B. Brown. Univ. Chicago Press, Chicago, Illinois. 1996: 566 pp. Cloth $95, Paper $34.95.—This monograph on the natural history and population dynamics of the Cliff Swallow is a summary of 12 years of study by Charles and Mary Brown at colonies in Keith County, Nebraska, in the Platte River Valley. It is an exploration of the phenomenon of coloniality, its costs, and its benefits. This is also a book that could be used as a model for those interested in monographic studies of behavioral ecology—although most researchers won't have the benefits that come with working with a species like the Cliff Swallow: large sample sizes, predictable and accessible nest sites, open habitat that is easy to work in, ease of manipulation, ease of capture, and plumage markings that lend themselves to unique color-marking schemes.

The Browns begin with a general chapter in which they provide the basics of Cliff Swallows and ask the questions that they focus on for the next 500+ pages. Yes, this is a long book—not an easy evening's read—or even an easy week's read. The major theme throughout the book is "the effect of group size on social behavior and demography" of nesting Cliff Swallows. Chapter 2 discusses techniques used, including adverse affects on the birds, and is a must for anyone contemplating work with this or similar species. Most adults were captured in mist nets, but for parentage studies, nests were plugged with cotton at night to capture both parents with their young. For studies of individual behavior, birds were uniquely marked with paint on their white forehead patch. Between 1982 and 1992, the Browns captured and banded 54,373 Cliff Swallows at their study sites.

Detailed experiments were focused on interplay between swallow and ectoparasite population dynamics. Incidence of ectoparasite infestations of birds increased through the nesting season. Substantial reduction of nestling mass and 50–100% nestling loss in larger colonies is attributed to the swallow bug (*Oeciacus vicarius*). Thus ectoparasites are a major cost of Cliff Swallow coloniality. Predation and responses of the birds to predators were also studied through monitoring and experimental manipulation (chapter 8), and preda-

tion losses were relatively greater at larger swallow colonies, thus again, coloniality is a liability. Evidence for information transfer among foraging birds suggests a benefit of coloniality, but greater brood reduction in larger colonies is suggested to be due to the birds having to travel farther to find food. Reproductive success (chapter 11) varied among years, but was generally greatest for colonies of 30–80 pairs. The Browns suggest this reflects the greater problems of ectoparasitism in larger colonies and the reduced foraging information transfer in smaller ones. Other chapters address nest-site competition (chapter 7), social foraging (chapters 9 and 10), and other factors affecting the birds. The social foraging chapters are detailed and fascinating, demonstrating the values of being a member of a flock for both predator avoidance and location of food. Chapter 12, on survivorship, sorts out many of these interactions. Chapter 14 addresses the evolution of coloniality, concluding that "Cliff Swallows initially formed breeding colonies to permit low-risk group foraging. The other benefits, and all the costs, of coloniality were automatic consequences."

The Browns' studies of these birds have also been reported in more than 20 journal articles. The elaboration here pulls it all together in one magnum opus. I congratulate them on a thorough and most useful book.—JEROME A. JACKSON.

THE MINDS OF BIRDS. By Alexander F. Skutch, illus. by Dana Gardener. Texas A&M University Press, College Station, Texas. 1996: xvi + 183 pp., 41 black-and-white drawings, one table. $29.95 (cloth).—More than a century ago C. Lloyd Morgan warned that "In no case may we interpret an action as the outcome of the exercise of a higher psychical facility if it can be interpreted as the outcome of the exercise of one which stands lower in the psychical state" (1896, *Introduction to Comparative Psychology,* Scott, London. p. 53). This principle has come to be known as Morgan's Canon and, for the most part, it has been diligently observed by mainstream science. In this new book, *The Minds of Birds,* Alexander Skutch challenges this dominant paradigm, suggesting that in the zeal to avoid the stigma of anthropomorphism, students of animal behavior have gone too far. Rather, if we recognize that humans and our avian relatives share both physiological homologies and life experiences, then it is parsimonious to attribute the specific actions of birds to human-like states and processes, such as consciousness, thought, and emotion.

The book is organized into 16 topical chapters, each designed to demonstrate how the mental capabilities of birds have been grossly underestimated. Chapter 1 addresses the extent to which birds recognize individuals of their own species, as well as individual human beings. Skutch introduces the topic by describing the many contexts in which individual recognition in birds is adaptive. He then illustrates the capabilities of birds with numerous examples from the literature, from stories related to him by his colleagues, and from his personal experiences. These accounts are both informative and entertaining. For example, he describes several instances where certain birds developed the habit of attacking particular humans while ignoring others. The attacking birds generally were not fooled when the targeted human exchanged clothing with a tolerated conspecific companion, suggesting that these birds recognized either facial characteristics or some other anatomical or behavioral features of their "enemies."

Chapter 2 deals with memory and expectation. Skutch presents numerous accounts of birds behaving contrary to the "widely held view that birds live only in the present, without conscious memories of the past or anticipation of the future." Many of the accounts are anecdotal, such as the behavior of a pair of Crimson-backed Tanagers (*Ramphocelus dimidiatus*) toward a snake near their nest; they continued to act in an agitated manner for a considerable time after the snake had been removed. The examples of caching behavior are more objective (e.g., corvids store up to 100,000 seeds with a recovery rate of 50–99%) and provide an impressive demonstration of avian memory.

Other chapters address social life, emotion, play, counting and timing, tool using, aesthetic sense, intelligence, freedom and altruism, and homing and migration. Another chapter is devoted to the apparent language skills of Alex, an African Gray Parrot (*Psittacus eri-*

thacus) who has been collaborating with Irene Pepperberg. A summary and concluding remarks are presented in the final chapter.

Although Skutch provides a wealth of information, much of it not previously available in the published literature, some readers undoubtedly will disagree with his interpretations of the data presented. For example, in Chapter 5, he concludes that birds, especially immatures, may sing for amusement or enjoyment alone, but he does not explore the possible selective advantages that a young male would gain by practicing and perfecting his species-specific vocalizations. Similarly, in the chapter on the emotions of birds, the tonal quality of calls elicited by the presence of an enemy are likened to those emitted by humans in similar circumstances, but the adaptive significance of wide-band dissonant alarm calls (vis-a-vis, high-frequency, narrow-band "seet" calls) is not discussed.

Skutch employs a comfortable writing style that will be accessible to both the scientific and lay communities. The attractive line drawings by Dana Gardener illustrate the species being discussed and effectively complement the text. The book is well produced; this reader found only a couple of typographical errors.

The objectives of *The Minds of Birds* are clear: to persuade the reader to reconsider the ability of birds to think and experience emotions, and to convince that reader that a bird's psyche is far more similar to that of a human than is generally regarded. Skutch succeeds with the former objective; this book is certainly thought-provoking. There will be a wide range of opinions in regard to the latter objective. For both reasons, I recommend this book.—JOHN A. SMALLWOOD.

PARTNERSHIPS IN BIRDS: THE STUDY OF MONOGAMY. Jeffrey M. Black, Ed. Oxford University Press, Oxford. 1996: 420 pp., 19 chapter heading drawings, numerous figures, graphs and tables. $55 (paper).—This book is a useful summary and analysis of some of the voluminous literature on mating systems in birds. As the subtitle indicates, the focus is on birds that are monogamous, but in the first chapter the editor points out that the whole concept of monogamy has changed drastically during the last few years—that we now realize that a female's choice of a breeding partner may be relatively unrelated to her choice of genes for her offspring. So the main question that the various authors consider is why and under what conditions monogamous social relationships persist. To understand this issue requires looking at the costs and benefits of social monogamy, and what factors constrain other options.

The first three chapters provide the theoretical framework for the examination of the case studies that follow. In chapter one the editor describes the working hypothesis of the book: that pair stability benefits individuals by increasing their ability to acquire resources for reproduction and survival. Furthermore, the relationship between pair members is viewed as dynamic; individuals are constantly reassessing the costs and benefits of staying and leaving. A brief description of the various hypotheses for why monogamy persists, and an overview of possible benefits and costs of staying with a breeding partner, follow. The chapter concludes with the guidelines followed by the contributing authors. This is helpful, since it means that the data for different species can be compared more directly than is usually possible.

In the second chapter the origin of mating systems is discussed, and a new hypothesis is proposed for the origin of social monogamy with genetic polygyny. The "constrained female hypothesis" considers mating partners as resources and looks at reproductive patterns in terms of animals manipulating their resources. This view suggests that when females are the limiting reproductive resource for males, males will be under strong selection to manipulate females. The ability of females to control their own reproduction, therefore, is critical to understanding the evolution of mating systems. This hypothesis differs from others in focusing on *female* quality, and the quality of the female's habitat. It suggests that high-quality females, or females in high-quality habitats, will be better able to resist male efforts, and therefore be able to control the level of extra-pair paternity. Such females will also be better able to rear offspring with little or no help from the male; thus they will suffer less if males decrease parental care as a result of decreasing certainty of paternity. Multiple

mating by females may arise, therefore, when females attempt to get the best genes possible under ecological or social constraints, and they can overcome males' efforts at manipulation.

In the final introductory chapter the relationship between monogamy and parental care is addressed. Specifically, the evolution of biparental care is seen as the key to understanding monogamy and this focus leads the authors to suggest that the structure of the family is the appropriate level of study. The authors suggest that simple mathematical modeling may be useful for making predictions which short-term experiments could test. This chapter shows how long-term data, such as those presented in the rest of the book, may be complemented by relatively simple, directed studies.

The 14 chapters making up the bulk of the book present case studies on a variety of socially monogamous birds, focusing on mate fidelity and the costs and benefits of divorce. While all of the species presented are socially monogamous, the entire spectrum of genetic contribution by the male is covered: from Bewick's swans where no extra-pair paternity is found, to promiscuous Splendid Fairy-wrens, where the majority of offspring result from extra-pair fertilizations. A good variety of species is covered—from the well known monogamous systems of ducks and swans, to perhaps lesser known systems such as penguins and ptarmigan.

The last two chapters summarize and synthesize the empirical data. Chapter 18 brings the discussion back to evolutionary forces—specifically the relationship between mate fidelity and sperm competition (both important aspects of mate choice) and sexual selection. The various hypotheses for the evolution of monogamy are reviewed and evaluated, with the constrained female hypothesis as the focus. The authors use the case studies and other examples from the literature to test this hypothesis. They conclude that their preliminary tests of the constrained female hypothesis look promising, but that more data and controlled studies are needed, especially in light of the great variability seen both among and within species. Finally, in the last chapter we revisit the basic question on which the book focused: Why do some monogamous birds remain faithful and others divorce? The authors summarize the empirical data presented earlier. They discuss the various mechanisms of pair formation and mate change, the costs and benefits of staying and leaving, the features of "good mates," and the importance of phylogenetic comparisons. They suggest that a comprehensive theoretical framework to explain mate fidelity and divorce is lacking, and they look to a recent mathematical theory as an important first step. Finally, they make suggestions for how future studies could further the field. This final chapter is a bit disappointing in its inability to draw far-reaching conclusions, but as the authors point out, this probably reflects our current lack of theory and, despite all of the long-term studies presented, appropriate data.

Overall this book will be a very useful reference for anyone interested in trying to wade through the empirical and theoretical literature regarding mating systems in birds. Although the theoretical chapters are rather heavy, they offer both a comprehensive review and some new insights. The species accounts provide an interesting look at one aspect of avian behavior, especially considering the long-term nature of these studies. Together these chapters present a complete review of monogamous mating systems in birds.—MARTA HERSEK.

Wilson Bull., 110(4), 1998, pp. 585–598

PROCEEDINGS OF THE SEVENTY-NINTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The seventy-ninth annual meeting of the Wilson Ornithological Society was held Monday, 6 April, through Sunday, 12 April, 1998, at the Regal Riverfront Hotel, St. Louis, Missouri, in joint session with the American Ornithologists' Union, the Association of Field Ornithologists, the Colonial Waterbird Society, the Cooper Ornithological Society, and the Raptor Research Foundation. The WOS having met previously with the AOU and COS in Montana in 1994, the current joint meeting shall be known as the Second North American Ornithological Conference. The Local Committee, co-chaired by Bette Loiselle and John Blake, included J. Katheryne Aldas, Ted Anderson, Sandra Arango, Nevin Aspinwall, Gilbert Barrantes, Paul Bauer, Louise Bradshaw, Carol Bourne, Godfrey Bourne, Lorena Calvo, Bruce Carr, Chris Collins, Walt Crawford, Michelle Crenshaw, Leslie Drewel, Rodney Dyer, Tibisay Escalona, Jeanne Fair, Jaqueline Goerck, Catherine Graham, Erpur Hansen, Jim Hunt, Seth Isenberg, Ivan Jimenez, Dave Klostermann, Randall Korotev, Michelle Land, Michael Macek, James Malone, Jaun Martinez, Patrick Osborne, Jorge Perez, Rachel Polster, Luis Miguel Renjifo, P. Mick Richardson, Bob Ricklefs, Grace Servat, Zuleyma Tang-Martinez, and Carolina Valdespino. The meeting was co-hosted by the University of Missouri at St. Louis, the Missouri Botanical Garden, the Saint Louis Zoo, Webster Groves Nature Study Society, the World Bird Sanctuary, Saint Louis University, and Washington University.

The Council met from 09:01 to 15:46 on Tuesday, 7 April, in Jefferson Room A of the Conference Center Area at the Regal Riverfront Hotel. At that time registration had already exceeded 1200. On Tuesday evening there was an informal dinner for Council, Fellows, and Board Members of the participating societies at the Top of the Riverfront restaurant, followed by an icebreaker reception for all in the Grand Ballroom.

The scientific program was organized by the Organizing Committee, which was chaired by Jeff Brawn and also included Ted Anderson, John Blake, Godfrey Bourne, Walt Crawford, John Faaborg, Jeanne Fair, John Kricher, Michelle Land, Bette Loiselle, Michael Macek, Robert Ricklefs, Scott Robinson, Kimberly Smith, and John Zimmerman. The scientific program comprised a total of 695 presentations, including four plenary lectures, 54 presentations in nine symposia, 490 papers in 49 general sessions, and 147 poster presentations. In addition, there were 10 workshops and one roundtable.

The opening session on Wednesday convened in the Grand Ballroom at 08:00 with welcoming remarks from Mike Scott, President of the Cooper Ornithological Society, and Ned Johnson, President of the American Ornithologists' Union, who introduced Chancellor Blanche Touhill of the University of Missouri at St. Louis. Following a welcome from Chancellor Touhill, Mike Scott introduced Peter Raven, Director of the Missouri Botanical Garden. Following Peter Raven's introductory remarks, Wilson Ornithological Society President Edward H. Burtt, Jr., introduced the second annual Margaret Morse Nice Plenary Award recipients, Ellen Ketterson and Val Nolan, Jr. The title of their lecture was "Studying birds: one species at a time."

Later that evening, the conferees were treated to the Flight Night Reception at the Saint Louis Zoo. Other receptions in the days to follow included the Student/Society Officer Mixer for students, post-docs, society officers, fellows, board and council members, and all other conferees, held in the Palm Court Lobby of the Regal Riverfront Hotel on Thursday, prior to the Poster Session and Reception held in the South Exhibit Hall. On Friday, those in attendance were the guests of the International Center for Tropical Ecology at UM-St. Louis and the Missouri Botanical Garden for a Tropical Night Reception at the Missouri Botanical Garden. Field trips during the week included excursions to Mingo National Wildlife Refuge, Duck Creek Conservation Area, Shaw Arboretum, Tyson Research Center, Riverlands Environmental Demonstration Area, Forest Park-Kennedy Forest, Tower Grove Park, Eagle Bluffs, a prairie chicken lek, Bradford Farm, St. Charles County-Busch Conservation Area, Mark Twain National Wildlife Refuge, and the World Bird Sanctuary.

On Saturday evening, following a social hour, the conferees assembled in the Grand Ballroom for the annual banquet. At the end of a satisfying meal, Bette Loiselle welcomed all, and introduced the Organizing Committee and society representatives. The following Wilson Ornithological Society awards were presented:

MARGARET MORSE NICE MEDALS (for the WOS plenary lecture)

Ellen Ketterson and Val Nolan, Jr., "Studying birds: one species at a time."

EDWARDS PRIZE (for the best major article in volume 109 of *The Wilson Bulletin*)

Richard H. Yahner, "Long-term dynamics of bird communities in a managed forested landscape." Wilson Bull. 109:595–613.

LOUIS AGASSIZ FUERTES AWARD

Jennifer A. Jacoby, "The genetics of reintroduced populations of an endangered bird, *Falco peregrinus*."

MARGARET MORSE NICE AWARD

David R. Fouts, "Towards a viable population of Purple Martins along the lower Columbia River: a study of artificial nesting habitat preferences."

PAUL A. STEWART AWARDS

Anna-Marie Barber, "Migration of passerines in interior Alaska."

Matthew A. Etterson, "Migratory status of Loggerhead Shrikes in southwest Oklahoma."

Andrew A. Kinsey, "Temporal and spatial variation in abundance of migratory birds at an inland stopover site on Kennesaw Mountain, Georgia."

Paul G. Rodewald, "Habitat use and selection by Neotropical migratory songbirds during migration."

Bonnie E. Stout, "Winter courtship and pair formation in grebes."

Selection committee for the Margaret Morse Nice Medals—Edward H. Burtt, Jr. (chair), John Kricher, and William E. Davis, Jr.; Edwards Prize—Charles Blem (chair), Robert Beason, Larry Clark, and Sara Morris; for the Fuertes, Nice, and Stewart Awards—Daniel Klem, Jr. (chair), Judith M. Rhymer, and Richard Stiehl. The Wilson Ornithological Society Travel Award and the Alexander Wilson Prize for the best student presentation were not awarded this year. Instead, student travel and presentation awards were decided jointly by the ad hoc Student Awards Committee, consisting of John Faaborg (chair), Kevin Brown, Carla Cicero, Maura Eagen, T. Luke George, Shannon Hackett, Patricia Hall, Eileen Kirsch, Daniel Klem, Rolph R. Koford, John Kricher, Elissa M. Landre, Mark Stanbeck, Kim Sullivan, Doris Watt, David F. Westneat, H. Herbert Wilson, and Petra Bohall Wood.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Burtt at 12:19 on Wednesday, 8 April, in the Missouri Ballroom. Secretary Smallwood then summarized what had transpired at Tuesday's Council meeting, remarking that over 1200 people had pre-registered for the Second North American Ornithological Conference, including 450 students, and that total registration would likely increase to about 1500. Secretary Smallwood informed those in attendance that the Josselyn Van Tyne Memorial Library needed to reduce its inventory of back issues of *The Wilson Bulletin*, and directed interested persons to contact the WOS website for more information. He then expressed the Society's gratitude to Bill Lunk, who had decided to resign after 40 years of service as the chair of the Library Committee. Secretary Smallwood highlighted the accomplishments of the Undergraduate Outreach Committee during the past year, under the leadership of Ernie Willoughby, including posting the "Guide to Graduate Programs in Ornithology" on the WOS webpage, submitting the report on undergraduate ornithology courses in North America (co-authored by Jed Burtt and Herb Wilson) to *The Wilson Bulletin*, another workshop on teaching ornithology (organized by Jed Burtt), and the production of an undergraduate ornithology lab manual (edited by Jed Burtt and John Faaborg). As Ernie had decided to retire from his chairmanship, those assembled offered him a round of applause for his contributions to the WOS. Secretary Smallwood then summarized the Council's discussion of the Conservation Committee report submitted by chair Jerry Jackson, which focused on the limitations of CITES. Next, he announced that Bob Beason had been reelected to his second year as editor of *The Wilson Bulletin*, and Bob was commended for successfully taking over the reins. Secretary Smallwood then noted that membership in the Society currently stood at 2365, including 294 student and 519 life members. The 1999 annual meeting will be held 10–13 June at Colby College in Waterville, Maine, at the invitation of Herb Wilson. Because of the June meeting date, Colby College will be able to provide affordable dormitory accommodations, and it is hoped that student attendance will be high. The 2000 annual meeting will be held in Galveston, Texas, from 26 (or 27) to 30 April, sponsored by the Houston Audubon Society and the Gulf Coast Bird Observatory; Dwight Peake will be the local host. Still in the early planning stages, the 2001 annual meeting will be held at the University of Arkansas sometime in April. The secretary then asked those assembled to stand in recognition of the following WOS members who had passed away since we last met: John J. Christian (Starlight, PA), John T. Emlen, Jr. (Madison, WI), Hildegard Howard (Los Angeles, CA), Margaret H. Hundley (Ellsworth, ME), Helen Lapham (Rock Island, RI), Mrs. Clark Miller (Inwood, WV), Laurie Muehlbach (Fresno, CA), Martin H. Moynihan (Canal Zone, Panama), Graham Netting (Rector, PA), Peter C. Petersen, Jr. (Davenport, IA), Thomas G. Scott (Fort Collins, CO), James B. Schuler (McClellanville, SC), Allen W. Stokes (Logan, UT), Miklos D. F. Udvardy (Sacramento, CA), Charles M. Weise (Milwaukee, WI), Nathaniel R. Whitney (Rapid City, SD), and Merrill Wood (Thompson, PA).

The treasurer's report was then offered by Doris Watt, after which Bob Beason delivered the editor's report.

Jerome A. Jackson, chair, presented the report of the nominating committee, which also included Mary H. Clench, Richard N. Conner, and William E. Davis, Jr., offering the following slate of candidates: President, Edward H. Burtt, Jr.; First Vice-president, John C. Kricher; Second Vice-president, William E. Davis, Jr.; Secretary, John A. Smallwood; Treasurer, Doris J. Watt; and Members of Council for 1998–2001, Jonathan L. Atwood and James L. Ingold.

The first business meeting was adjourned at 12:51.

SECOND BUSINESS MEETING

The second business meeting was called to order by First Vice-president John Kricher at 12:05, Friday, 10 April, in the Missouri Ballroom. As the first item of business, he asked Secretary Smallwood to read aloud the following:

COMMENDATION

WHEREAS the Wilson Ornithological Society held its annual meeting in St. Louis, our nation's historic gateway to the west, in an historic joint conference with the American Ornithologists' Union, the Cooper Ornithological Society, the Association of Field Ornithologists, the Raptor Research Foundation, and the Colonial Waterbird Society, under the appellation "1998 North American Ornithological Conference"; and

RECOGNIZING that the Committee on the Scientific Program, consisting of members of each of the participating societies and skillfully chaired by Jeff Brawn, organized a remarkable schedule of oral and poster presentations into a momentous number of general sessions, symposia, and workshops; and

RECOGNIZING that the Committee on Local Arrangements, under the able direction of co-chairs Bette Loiselle and John Blake, through the efforts of members of the Department of Biology and International Center for Tropical Ecology at the University of Missouri-Saint Louis, the Saint Louis Zoo, the Saint Louis Audubon Society, the Webster Groves Nature Study Society, the World Bird Sanctuary, the Missouri Botanical Garden, Washington University, Saint Louis University, and McKendree College, provided an outstanding conference venue at the foot of the historic Gateway Arch National Monument; and

WHEREAS those attending experienced a most enjoyable and informative conference;

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commend the Committee on the Scientific Program, the Committee on Local Arrangements, and the local sponsors for an especially successful and rewarding meeting in Saint Louis.

The motion to accept this resolution was made by Ted Davis and seconded by Sara Morris, after which it passed unanimously.

First Vice-president Kricher then recalled the report of the nominating committee to the floor. Jerome A. Jackson, chair, invited additional nominations from those assembled. Hearing none, Dick Banks moved and Dick Conner seconded that the nominations be closed. Dick Banks then moved that the secretary cast a unanimous ballot for all offices. Following a second by Mary Clench, and the unanimous approval of those assembled, he did so.

The following resolutions were drafted by the 1998 North American Ornithological Conference Resolutions Committee, which included David Blockstein (chair), Amy-Mathews Amos, Tom Bancroft, Mary Beth Beetham, Rebekah Creshkoff, Jerry W. Davis, Bill Evans, Kimball Garrett, Frank Gill, Jim Greaves, Evan Hirsche, Joe Jehl, Daniel Klem, Jr., Suellen Lowry, Kathy Molina, Ellen Paul, C. J. Ralph, Martin Raphael, Stan Senner, Kim Smith, Pepper Trail, and Gerald Winegrad, and were presented by David Blockstein. As a group, they passed unanimously.

EXXON VALDEZ RESTORATION RESERVE FUND

WHEREAS in the court settlement following the Exxon Valdez oil spill, a trust fund was established to provide for restoration and enhancement of resources injured as a result of the spill and a trustee council was created to oversee the allocation of that money with a mission to return the environment to a "healthy, productive, world-renowned ecosystem"; and

WHEREAS the impact of the spill was primarily on the marine ecosystem and its inhabitants, including Common Murres (*Uria aalge*), Thick-billed Murres (*Uria lomvia*), Pigeon Guillemots (*Cepphus columba*), Marbled Murrelets (*Brachyramphus marmoratus*), cormorants (*Phalacrocorax* spp.), and other seabirds; and

WHEREAS more than half of the money available for restoration has been spent on land purchases to protect valuable fish and wildlife habitats, not all of which will directly improve the marine resources damaged by the spill; and

WHEREAS the Trustee Council previously established a Restoration Reserve account to provide funds for restoration activities after the last Exxon payment in 2001; and

WHEREAS in adopting the restoration plan, the Trustee Council specifically recognized that monitoring recovery, understanding the spill's effects on the ecosystem and undertaking needed restoration activities "on an ecosystem basis" will extend well into the future; and

WHEREAS by 2001, the reserve fund is expected to total about $140 million, including interest; and

WHEREAS the Trustee Council will make a decision in 1998 on the allocation of that fund; and

WHEREAS scientific research is necessary for an understanding of the northern Gulf of Alaska ecosystem, which has not been well studied (for example, there is a need for increased understanding of the interrelationships among seabird colonies and their dependence on poorly-studied forage fishes in the region); and

WHEREAS use of the information based on research is essential for protecting the marine resources of Prince William Sound and the northern Gulf of Alaska; and

WHEREAS only through continued research and monitoring will it be possible to determine the long-term effects of the spill and of the measures used to mitigate those effects; and

WHEREAS the chief scientist of the Trustee Council has proposed using the reserve fund to establish a permanent, adaptive, interdisciplinary research and monitoring program, which "would track, and eventually predict, ecosystem changes and provide a basis and mechanism for long-term restoration, enhance-

ment, and wise management of marine resources in the northern Gulf of Alaska";

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society encourage the Exxon Valdez Trustee Council to (a) establish a permanent fund for competitive, peer-reviewed research and monitoring of the northern Gulf of Alaska ecosystem and (b) allocate all or nearly all of the restoration reserve fund for this purpose; and

THEREFORE BE IT FURTHER RESOLVED that an ongoing marine conservation biology research and monitoring program should be based on the following core principles:

1. Research and monitoring should focus on conserving and recovering the living marine resources and biological diversity of the Gulf of Alaska, and should be coordinated with other federal and state marine research programs in Alaska, such as those in the Bering Sea, to leverage efforts and enhance the benefits of each.
2. Decisions on research and monitoring proposals should be based on a competitive scientific peer review process involving not only Alaskan scientists, but a mix of scientists throughout the United States with appropriate expertise in the various research topics to be considered. The best science results from involving the most appropriate scientists in all aspects of the process, and from basing funding decisions on emerging scientific and management questions. The resulting science should be of sufficient quality for publication in the best scientific journals.
3. The overall design of the long-term monitoring and research program should be reviewed by the National Research Council, the National Science Foundation, or other appropriate scientific bodies.
4. Research and monitoring should be ecosystem-oriented, designed and implemented to understand the processes and relationships governing marine ecosystem functioning, to enhance recovery of living marine resources that were harmed by the Exxon Valdez oil spill or are otherwise in decline, and to address emerging environmental problems and biodiversity loss in the Gulf of Alaska.
5. Research and monitoring should not be narrowly focused on maximizing certain resources for short-term economic gain, but should be broad-based and seek to understand how marine ecosystems function as a basis for management and conservation in the long run.
6. Use of indicator species is appropriate in some cases; however, in addition to studies on specific species, integrative research should be conducted to tie together information through modeling and other techniques to develop an understanding of processes affecting species on large geographic and temporal scales.
7. Research and monitoring projects should include long-term studies, allowing observation of environmental variation over decades to increase scientific understanding of ecosystem processes that vary over long time periods, and enhance our understanding of natural vs. human-caused environmental changes.

NATIONAL FOREST MANAGEMENT, FOREST HEALTH AND ROADLESS AREAS

WHEREAS America's national forests are comprised of 156 separate forests, encompassing 25 percent of all federal public lands (200 million acres), providing essential habitat for many bird species and other biota, including a greater number of threatened and endangered species than on any other system of federally owned land; and

WHEREAS the remaining large, unfragmented, roadless areas provide particularly important and irreplaceable habitat for many species, and such areas are found almost exclusively on national forests and other public lands; and

WHEREAS many of America's national forests are overcut and fragmented due to excessive logging; and

WHEREAS few roadless areas are protected (for example, in the Blue Mountains of eastern Oregon and Washington, less than 8% of 722,000 acres of forested roadless areas are administratively protected); and

WHEREAS the Clinton Administration is attempting to implement policy to favor conservation based on the capacity of the land; and

WHEREAS elements of this policy include a proposed 18-month moratorium on logging in large roadless areas (greater than 5000 acres) in most national forests; and

WHEREAS the proposed moratorium is consistent with the recommendations of the Eastside Forest Scientific Society Panel (Interim protection for late-successional forests, fisheries and watersheds; The Wildlife Society Technical Review 94–2, 1994), in which the American Ornithologists' Union was a participant; and

WHEREAS there is considerable effort in Congress to oppose Administration policy and allow more logging under the guise of a so-called "forest health crisis"; and

WHEREAS the American Ornithologists' Union and the Cooper Ornithological Society have each passed resolutions challenging the scientific basis of the "forest health crisis";

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society support the efforts of Forest Service Chief Michael Dombeck and the Clinton administration towards increasing conservation and protection of roadless areas in national forests; and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society urge the Clinton ad-

ministration to extend these roadless area protections to all national forests and to roadless areas of 1000 acres or more; and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society oppose Congressional attempts to increase logging of national forests under the guise of a "forest health crisis" and urge Congress to take steps to prevent loss and fragmentation of roadless areas.

FUNDING FOR NATURAL RESOURCE SCIENCE

WHEREAS scientific knowledge is a necessary basis for effective management of natural resources; and

WHEREAS present knowledge of the natural resources of the United States is insufficient for many management objectives to be achieved; and

WHEREAS current federal funding for biodiversity and ecosystems research and monitoring (estimated at $460 million by the National Science and Technology Council) is inadequate to meet the needs of resource managers and decision makers; and

WHEREAS the proposed fiscal 1999 budget of $158 million for the Biological Resources Division (BRD) of the U.S. Geological Survey is less than its budget for fiscal 1994 ($164 million) before the 104th Congress imposed an 15% cut when BRD was an agency known as the National Biological Service; and

WHEREAS budget restrictions on BRD allow it to accomplish relatively few priorities identified by other agencies in the Interior Department, leaving the U.S. Fish and Wildlife Service with a list of some 300 unaddressed research needs, and have caused a 40% decrease in BRD maintenance activities and no new construction since fiscal 1994; and

WHEREAS the research budget of the U.S. Forest Service has remained essentially flat since a 5% recision in fiscal 1995 and research is now at about 7% of the agency budget rather than the 11% that has been traditional; and

WHEREAS neither President Clinton's 21st Century fund for research nor Senator Gramm's National Research Investment Act of 1998 (S. 1305) include science in the natural resource agencies and departments among their significant proposed increases in science funding; and

WHEREAS a 1998 report of the President's Council of Advisors on Science and Technology ("Teaming with life: investing in science to understand and use America's living capital") recommends increases of up to $200 million annually (phased in over three years) for research, education, management and information infrastructure necessary to make sustainable use of biodiversity and ecosystems;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society encourage the President and the Congress to significantly increase funding for natural resource science and related activities in agencies including the U.S. Geological Survey (particularly the Biological Resources Division), the U.S. Forest Service, and the proposed National Institute for the Environment (NIE) under the National Science Foundation.

IZEMBEK NATIONAL WILDLIFE REFUGE

WHEREAS the Izembek National Wildlife Refuge (INWR) and the Izembek Lagoon (Izembek State Game Refuge) it encompasses, located on the Alaska Peninsula, is so important as wetland habitat for wildlife diversity that it was recognized as the first wetland site in the United States placed on the list of wetlands of international importance under the "Ramsar" Convention; and

WHEREAS the refuge and the lagoon are being considered for additional international recognition as a reserve of international importance by the Western Hemispheric Shorebird Reserve Network; and

WHEREAS the refuge provides habitat for numerous bird species, including a resident, non-migratory Tundra Swan (*Cygnus columbianus*) population, approximately half the world population of the threatened Steller's Eider (*Somateria fischeri*), the entire Pacific Brant (*Branta bernicla*) population, and the entire population of Emperor Geese (*Chen canigica*); and

WHEREAS the refuge's Kinzarof Lagoon has the only significant eelgrass (*Zostera marina*) beds on the Pacific side of the Alaska Peninsula, which is a primary food source for numerous bird and fish species; and

WHEREAS two identical bills, S. 1092 and H.R. 2259, are presently before Congress, each of which has been passed by committees in their respective houses, which would direct construction of a road that would traverse seven miles of the Izembek Wilderness and four more miles of the refuge, and bisect an isthmus between the Izembek and Kinzarof Lagoons; and

WHEREAS the bills suspend the application to the road project of all environmental laws, including the Endangered Species Act, Migratory Bird Treaty Act, and all federal provisions to protect wetlands and to require environmental impact assessments; and

WHEREAS the proposed road through this fragile tundra is likely to: degrade wilderness values; increase silt loads to the lagoon and/or decrease fresh-water flow to the lagoon, which could affect eelgrass growth and production; disturb wildlife, including the many birds in the area and result in increased pressure from future human disturbance; expose the Izembek Lagoon to waterborne contaminants from shipping accidents or potential offshore oil development; and

WHEREAS Congress designated 95% of the INWR as wilderness in 1980, and the Wilderness Act prohibits the building of permanent roads within any wilderness areas;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society urge Congress to reject S. 1092

and H.R. 2259 and to oppose any other effort to build a road through the Izembek National Wildlife Refuge.

NORTHEAST NATIONAL PETROLEUM RESERVE

WHEREAS the Northeast National Petroleum Reserve ("the Reserve") is a low-lying coastal region comprising nearly 4.6 million acres of nearly undisturbed foothill tundra and wet tundra; and

WHEREAS the Reserve encompasses the largest stretch of low-lying, coastal plain tundra and foothill tundra in Alaska, and perhaps in North America; and

WHEREAS the ecosystems and habitat represented in the Reserve are not found in protected areas in Alaska; and

WHEREAS numerous bird species are found in the Reserve, including the Yellow-billed Loon (*Gavia adamsii*) and Gyrfalcon (*Falco rusticolis*), which nest only in this region in the United States, the threatened Spectacled Eider (*Somateria fischeri*) and Steller's Eider (*Polysticta stelleri*), molting waterfowl, and large populations of many shorebirds and waterbirds; and

WHEREAS the Colville River Special Area of the Reserve has been recognized as one of the most significant regional habitats for raptors in North America, including nearly 90 nesting pairs of Peregrine Falcons (*Falco peregrinus*), which have only recently returned to this area following the DDT-caused decline in the 1970s; and

WHEREAS The Bureau of Land Management is considering an Integrated Activity Plan for the Reserve, with five alternative courses of action, each making a certain amount of the Reserve available for gas and oil extraction activities; and

WHEREAS the Draft Environmental Impact Statement analyzing each of these alternatives is inadequate in that it fails to evaluate adequately the unique ecological and biological features of the reserve, and fails to address available literature on the response of bird populations to various types and levels of development; and

WHEREAS there has not been adequate surveying of the presence and abundance of the bird species found in the region;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society recommend that the Bureau of Land Management defer the selection of a management plan for the Reserve until basic surveys and research have been completed, or, if deferment is not possible, that the Bureau of Land Management select Alternative A, the "no action" alternative which will continue the current management and allow no oil or gas leases; and

THEREFORE BE IT FURTHER RESOLVED that whatever management plan is selected by the Bureau of Land Management, that it be implemented in such a manner as to include very specific safeguards, based upon scientific information, to protect the environment and the wildlife found within the Reserve.

THE PUBLIC LANDS FUNDING INITIATIVE

WHEREAS America's public lands, wildlife, fish, and plants are irreplaceable natural assets that belong to, and benefit, our entire nation; and

WHEREAS the ideals underlying the creation and protection of our parks, refuges, forests, and other national lands have been admired and emulated around the world; and

WHEREAS these public lands represent an investment in America through the conservation of our natural and cultural heritage; and

WHEREAS more and more Americans are turning to our public lands for education, recreation, and the economic well being of their families and communities; and

WHEREAS ironically, at the same time that these assets are increasing in value, their vitality is threatened by inadequate funding and shortsighted investment in the agencies that care for them; and

WHEREAS the account in the federal budget that pays for the care and upkeep of our public lands (Function 300—Natural Resources and Environment) is slated to decrease over the next five years under the Balanced Budget Agreement; and

WHEREAS the financial condition of our public land and natural resource management agencies is in crisis and without significant increases to base funding over the next five years, these agencies and programs will be unable to protect and manage the resources entrusted to their care;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society support the Public Lands Funding Initiative, including the following proposed funding increases that are based on data requested from the agencies, and reflect real need:

- The Fish and Wildlife Service, $710 million to operate the National Wildlife Refuge System, to implement the Endangered Species Act, and for migratory bird management.
- The National Park Service, $630 million for natural and cultural resource protection, park operations, and maintenance of physical infrastructure.
- The Bureau of Land Management, $125 million for wildlife, fisheries, and threatened and endangered species, to provide recreational opportunities, and for paleontology research. (Note: the request for BLM is well below needs for adequate stewardship of its 260 million acres. This request is based on amounts that could be used effectively with limited or no increases in staff.)
- The Forest Service, $618 million for Fish, Wildlife, and Rare Plants; Recreation; Wilderness; Road Obliteration and Maintenance; Invasive Species; Rangeland Management; and Research on Wildlife, Fish, Water and Air.
- The U.S. Geological Survey's Biological Resources Division, $185 million for biological research, re-

source monitoring, information transfer, and maintenance and operations of research laboratories, cooperative research units; and their equipment.

- The Land and Water Conservation Fund, at least $700 million (assuming the base does not include the additional $699 million in FY98) to achieve full funding for land acquisition needs in the four agencies and to revitalize the grants to states and local communities for recreation and open space needs.

RESOLUTION IN SUPPORT OF THE SALTON SEA AS A SIGNIFICANT WILDLIFE HABITAT

WHEREAS the Salton Sea, the third largest interior saline lake in North America, formed by accidental water diversions from the Colorado River into southeastern California in 1905–6 and presently maintained by inflows of water imported for agricultural purposes, agricultural runoff, and freshwater river flows, has long been recognized as providing significant wetland habitat for a highly diverse array of migratory and breeding waterbird populations; and

WHEREAS recent surveys have revealed populations of up to 1.5 million Eared Grebes in midwinter (Jehl 1988), up to half of California's wintering White-faced Ibis (Shuford et al. 1996), and regional significance as an integral component of the Pacific Flyway for tens of thousands of migratory shorebirds (Page et al. 1992), waterfowl, and American White Pelicans, as well as significant breeding colonies of Double-crested Cormorants and Caspian Terns (K. Molina unpubl. data), nearly 40% of the nesting Black Skimmers (Collins and Garrett 1996), and by far the larger of only two breeding populations of Gull-billed Terns in western North America (Parnell et al. 1995); and

WHEREAS the Salton Sea has been documented to be of significant value as avian habitat from the time of its formation (see, for example, early studies reported by Grinnell 1908, Dawson 1923, Pemberton 1927, Miller & van Rossem 1929), and has retained this significance in the subsequent nine decades, with the Sea and its surrounding agricultural lands remaining a renowned birdwatching locality of national significance with over 350 species recorded and immense numbers of breeding, migrant, and wintering birds, in addition to unique post-breeding use by a variety of subtropical waterbirds; and

WHEREAS the Salton Sea represents a complex mosaic of habitats and land-use types, from saline lake waters to brackish and freshwater deltas resulting from both natural and imported (agricultural) water sources, and of state and federal wildlife refuges, agricultural areas, and geothermal developments, all with equally complex interactions and often competing interests; and

WHEREAS the State of California and surrounding regions have experienced significant losses of wetlands (Johnson and Jehl 1994), including coastal wetlands, interior wetlands (most notably the Colorado River delta and Tulare Lake basin), and interior saline lakes such as Owens Lake (Jehl 1994), making the Salton Sea, despite its "artificial" genesis, especially unique and important as de facto mitigation on a regional if not continental scale; and

WHEREAS significant colonies of ground-nesting colonial waterbirds and herons, as well as of the recently established Brown Pelican, have thrived during the 1990s, likely due in large measure to decreased levels of human recreational uses of key portions of the Salton Sea (Molina 1996); and

WHEREAS the Salton Sea has experienced high levels of eutrophication, salinization, and contamination, resulting in diminished water quality (Setmire et al. 1990); and

WHEREAS freshwater sources for the Salton Sea are currently under threat from planned diversions to coastal urban regions of California; and

WHEREAS there have recently been large-scale mortalities of birds (150,000 Eared Grebes in 1992, 1400 Brown Pelicans in 1996, many nesting Double-crested Cormorants in 1997) and millions of fish, all symptomatic of severe problems in the ecosystem; and

WHEREAS current attempts by agencies, NGOs, private concerns, and lawmakers to "save" the Salton Sea are gaining momentum, including engineering studies, Congressional legislation, and an Environmental Impact Statement together with a scientific review committee conducted by the Department of the Interior; and

WHEREAS there is no consensus on what is meant to restore or "save" the Salton Sea;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society recognize the significance of the Salton Sea to wildlife and support rehabilitation and conservation efforts for the Salton Sea that are responsive to the needs of wildlife and based on sound and thorough biological data; that recognize the importance of freshwater, delta, brackish, saline, and agricultural habitats at the Salton Sea; that improve water quality and guarantee continued adequate sources of freshwater; that stress the critical need for protection and isolation of waterbird colonies from human and other disturbance; and that seek to minimize threats to wildlife potentially resulting from urban and recreational development; and

THEREFORE BE IT FURTHER RESOLVED THAT the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society support an approach that allows sufficient time to study the situation, including all feasible options, that any additional research funds are added to agency core budgets, that no money be spent on "emergency action" before a full environmental impact statement is completed, including studies of the impacts of brine or salt disposal from all pumped water, and that the implementation of whatever action be recommended must meet all environmental laws, including the National Environmental Policy Act and the Clean Water Act, and that judicial review of proposed actions be allowed without restraint.

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SNOW GOOSE POPULATION MANAGEMENT

WHEREAS an exponentially growing population of lesser Snow Geese (*Chen caerulescens*) breeding along the border of Hudson Bay and migrating through mid-continental North America is overgrazing and overgrubbing its breeding habitat, causing changes in vegetation and soil salinity and threatening large portions of the Arctic ecosystem with potentially irreversible ecological degradation; and

WHEREAS plant species grubbed and eaten by the rapidly growing Snow Goose population in the Arctic are being destroyed to an unprecedented extent, and are being replaced over vast areas by unpalatable, salt-tolerant species; and

WHEREAS extensive scientific research on the effects of Snow Geese, including long-term exclosure experiments, suggests that their alteration of the biotic environment, especially plant community composition and structure, and the abiotic environment, especially soil chemistry, may be irreversible; and

WHEREAS long term studies show that populations of many bird species that depend on tundra habitat are declining precipitously as Snow Goose populations have grown and there is a concern that these declines may be linked to the growing Snow Goose population (these declining populations include species such as Hudsonian Godwit, Smith's Longspur, Yellow Rail, American Golden Plover, and Stilt Sandpiper, and a host of more widespread species with substantial numbers potentially at risk); and

WHEREAS the rapid increase in mid-continent Snow Goose populations is primarily a result of human modifications of habitat on the wintering grounds, along the migratory routes, and in the staging areas; and

WHEREAS the habitat modifications promoting population growth of Snow Geese include modern and large-scale agricultural practices throughout the nonbreeding range, and these conditions are likely to persist for many decades; and

WHEREAS scientific evidence indicates that a continued growth of the mid-continent Snow Goose populations threatens the integrity of important wildlife habitat, including managed refuges, waterfowl wintering grounds, and key migratory resting and staging areas in the United States; and

WHEREAS density dependent population control mechanisms will not self-regulate the exponential population explosion of Snow Geese because of the species' demonstrated ability and willingness to extend both nesting and foraging ranges continually into new areas as the existing breeding grounds become degraded; and

WHEREAS the mortality of adult geese is viewed as the driving demographic variable by which humans can hope most effectively to reduce the total population, its rate of growth, and its effects on the environment; and

WHEREAS the 1997 report entitled "Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group" has been published by the Arctic Goose Joint Venture (AGJV) Management Board and Working Group (under the auspices of the North American Waterfowl Management Plan), has received adequate peer review, and concludes with a series of specific recommendations to reduce Snow Goose numbers;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society endorse the science-based recommendations of the Arctic Goose Habitat Working Group as necessary steps for reducing mid-continent Snow Goose numbers "to a level of about 50% of

current numbers by the year 2005" (1997, Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group, p. 118); and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society recommend that the Arctic Goose Habitat Working Group and other appropriate organizations identify and develop solutions to the anthropogenic changes in environmental conditions that have led to the problem.

COMMUNICATION TOWERS AND AVIAN MORTALITY

WHEREAS an estimated two million to four million birds are killed in collisions with communication towers, particularly those higher than 200 feet, in eastern North America alone each year; and

WHEREAS towers 200 feet and taller are required to be lit for aircraft safety, generally with blinking lights; and

WHEREAS birds migrating at night are attracted by the light and circle the tower, striking supporting guy wires; and

WHEREAS there are presently at least 75,000 towers above 200 feet tall in the U.S. (according to the Federal Aviation Administration) and another 100,000 are expected to be constructed in the next decade (according to the communications industry) due to expansion in various communications markets, and to accommodate digital TV; and

WHEREAS the accrued impact of thousands of towers on migrant songbird populations may be significant for declining species such as Cerulean Warblers and endangered species such as Kirtland's Warbler;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society urge the Federal Aviation Administration (FAA) to endorse studies involving experiments toward finding lighting systems for towers that reduce avian mortality; and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society encourage the communications industry to voluntarily reduce the number of new towers by co-locating new transmitters on existing towers and to work with the U.S. Fish & Wildlife Service (USFWS) to minimize collisions of birds with towers; and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society strongly encourage the USFWS to work with the FAA and the Federal Communications Commission to study the magnitude of the problem, including thorough preparation of an Environmental Impact Statement, and to develop a national plan to minimize collisions of birds with towers.

DESIGN OR MODIFICATION OF BUILDINGS AND OTHER STRUCTURES TO REDUCE COLLISIONS BY BIRDS

WHEREAS birds are often unable to recognize sheet glass as a barrier, and at least 100 million to a billion birds are killed each year in the United States alone by striking glass of various sizes, in all types of human-built structures, during every season; and

WHEREAS the lights in tall lighted structures such as those in multistory buildings are known to disorient and result in bird fatalities from colliding with windows and opaque walls; and

WHEREAS glass can be modified to transform it into barriers that birds can recognize and avoid; and

WHEREAS the enactment of a building policy of minimum night lighting, especially during migration, can markedly alleviate bird attraction and confusion around tall buildings and towers; and

WHEREAS the problem of collisions between birds and windows is ubiquitous, incremental, cumulative, insufficiently documented and not well recognized as to its magnitude or its parameters; and

WHEREAS there has been insufficient research on building design and placement, alternative materials, landscaping and other measures to minimize collisions;

THEREFORE BE IT RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society encourage the U.S. Fish and Wildlife Service, as custodians of the nation's migratory bird resource, to make research related to bird-window collisions and their avoidance high on its priority list and to encourage the Biological Resources Division of the U.S. Geological Survey to carry out the needed research; and

THEREFORE BE IT FURTHER RESOLVED that the American Ornithologists' Union, Association of Field Ornithologists, Cooper Ornithological Society and Wilson Ornithological Society encourage the American Bird Conservancy to undertake a campaign, similar to its "Cats Indoors" campaign to raise awareness of the issue and to work with glass manufacturers, architects, builders, developers, landscape planners, building managers and home owners to find ways to reduce the problem of unintentional killing of wild birds in collisions.

A brief discussion on the merits and disadvantages of "mega-meetings" such as the North American Ornithological Conference followed passage of the resolutions. As there was no other business brought to the floor, Ken Parkes moved and Ted Davis seconded that the second business meeting be adjourned. All in agreement, it happened at 12:12.

REPORT OF THE TREASURER
1 July 1997 to 1 July 1998

GENERAL FUNDS

Balance Forward		$ 95,026.74
Receipts		
Regular and Sustaining Memberships	$ 31,850.00	
Student Memberships	$ 4,494.00	
Family Memberships	$ 186.00	
Total Dues		$ 36,530.00
Subscriptions	$ 26,350.00	
Newsletter	$ 244.80	
Back Issues	$ 399.00	
Page Charges	$ 18,033.50	
Total Income from Publications		$ 45,027.30
Contributions: Research Fund	$ 381.00	
Van Tyne Library	$ 717.00	
General Endowment	$ 88.00	
Life, Patrons (Gen Endowment)	$ 2,000.00	
Unrestricted	$ 1,025.00	
Total Contributions		$ 4,211.00
Royalties	$ 1,451.60	
Interest from Checking Account	$ 1,020.69	
Interest from Endowments	$ 24,937.90	
Dividends from Dreyfus Acct (reinvested)	$ 1,044.86	
Subtotal		$ 28,455.05
Miscellaneous		$ 552.00
Net OSNA Adjustment		$ (1,140.61)
TOTAL RECEIPTS		$113,634.74
Disbursements		
Bulletin Publication		
March 1997	$ 18,064.23	
June 1997	$ 16,825.66	
September 1997	$ 18,556.58	
December 1997	$ 22,550.50	
March 1998	$ 17,754.76	
Editorial expenses	$ 8,046.26	
Total Publication Costs		$101,797.99
OSNA Expenses	$ 9,702.00	
Flock	$ 187.15	
Officer's expenses	$ 869.67	
CPA (tax filing)	$ 430.00	
Incorporation fee	$ 5.00	
Editor's honorarium	$ 2,000.00	
Editor's travel	$ 500.00	
Nice speaker expenses 1997	$ 1,060.00	
Nice speaker expenses 1998	$ 830.34	
Plaque/Medal costs	$ 2,765.00	
Total Operating Expenses		$ 18,349.16
Organizational Awards	$ 3,000.00	
Ornithological Council Contribution	$ 1,000.00	
ABC & NABC Dues	$ 250.00	
Total Philanthropies		$ 4,250.00
SUBTOTAL DISBURSEMENTS		$124,397.15

Transfer to Mellon Account		$ 20,000.00
TOTAL DISBURSEMENTS		$144,397.15
Ending Balance		$ 64,264.33

CASH ACCOUNTS

First Source Bank Checking 1 July 1998	$ 42,601.19	
Dreyfus Liquid Assets 1 July 1998	$ 21,663.14	
Total Cash on Hand		$ 64,264.33
Van Tyne Library Accounts		
Starting Balance	$ 3,100.98	
Receipts	$ 963.59	
Expenses	$ 1,927.54	
Ending Balance		$ 2,137.03

SUTTON DESIGNATED ACCOUNTS

Endowment Principal as of 1 July 1997	$ 66,357.54	
Increase in Principal Value 1996–1997	$ 79,931.00	
1997 Earnings*	$ 2,318.00	
Costs for Color Plates (3)	$ 3,007.03	
Balance		$ (689.03)

TOTAL ENDOWMENT FUNDS

1996 Market Value	$676,029.00
1997 Market Value	$814,315.00
1998 Market Value (1 July 1998)	$968,838.00

* Based on 2.9% yield on Mellon account

Doris J. Watt, *Treasurer*

EDITOR'S REPORT—1997 (May–December)

Between 1 May and 31 December 1997, the editorial office of *The Wilson Bulletin* received 182 manuscripts including 17 that were forwarded by the previous editorial office with reviews. This is above the 10-year average of 175/year reported by Charles Blem, the previous editor, but similar to the 1996 total of 200 manuscripts. The acceptance rate was 42% for these manuscripts, slightly higher than the 36% for 1996. Most of manuscripts were returned to the authors with reviewers' comments within three months and many within two months. A few manuscripts required 4–6 months before a decision could be made about their acceptance; invariable because of difficulties in finding appropriate reviewers or obtaining reviews from delinquent reviewers. We have been using E-mail for much of the correspondence with authors and reviewers. This has resulted not only in monetary savings from postage, but also has resulted in faster turn around for manuscripts; in some cases the author received a decision within a month of submission.

As a result of the new format and page size of *The Wilson Bulletin,* the journal has gone from approximately 200 pages per issue to 150 pages. The current issues contain the same number of manuscript pages, figures, and tables as previous issues. Most of the difference in length is because many of the figures and tables require less space with the 2-column format than they did with the single column format. The result has been a savings in printing charges (estimated at $2000) to produce the journal. A second source of savings has been the use of electronic manuscript submission. All of the authors for the first two issues of volume 110 have provided disk or E-mail submission of their final manuscripts. Although it has made for more work by the editorial office to edit these files, the benefits to the society are cost savings of about $6.00 per page ($900 for the issue) and, more importantly, the retention of all the proof reading that has been invested into the manuscript.

I greatly appreciate the assistance of Charles Blem, the previous editor, for his advice and encouragement, especially during the early months of my editorship. Kathy G. Beal has provided timely advise on many manuscripts, especially those with difficult statistical problems. Editorial assistants Tara Baideme, Melanine Daniels, and Dante Thomas assisted in editing and checking many of the manuscripts that were accepted for publication. Tara Baideme provided much of the work in setting up the editorial office, tracking manuscripts, and correspondence. Tara Schuley and numer-

ous other people at Allen Press were extremely helpful in developing the new style for the journal. The State University of New York at Geneseo and the Biology Department continue to support the editor and the running of the editorial office in many ways. As a new editor, I especially welcome suggestions and feedback on how to improve service to the authors and the membership as a whole.

Robert C. Beason, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

The WOS Membership Committee consists of Laurie Goodrich at Hawk Mountain Sanctuary, Jim Ingold at Louisiana State University, Mark Woodrey at the Mississippi Museum of Natural Science, Mary Clench of Gainesville, Florida, and myself, at Montclair State University in New Jersey.

Laurie Goodrich continues to handle the arrangements for making the WOS recruitment poster available at ornithological meetings. This past year the poster was displayed at the WOS meeting in Manhattan, Kansas; the American Ornithologists' Union meeting in Minneapolis, Minnesota; and the Raptor Research Foundation meeting in Savannah, Georgia. At each venue WOS membership brochures are made available; our supply of brochures appears to be sufficient for another year.

Jim Ingold continues to contact nonmembers who make presentations at the annual meetings.

During the past year I received only a few letters from people interested in joining the WOS, and I responded to each by sending the WOS membership brochure and a personal letter of welcome to our society. Having completed my eighth year of chairing the Membership Committee, I have decided that this is an appropriate time to pass the reins on to a new chair. I am very grateful for the opportunity I have had to participate in the society in this manner. I forwarded to President Burtt my nomination of Laurie Goodrich to be the new committee chair, as she has been doing the committee's heavy lifting (literally) for the past two years. I am pleased that she will begin her duties as chair at the 1998 annual meeting. The Membership Committee will be in very good hands.

John A. Smallwood, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Another year in the long history of the Society has, as usual, meant a year of hard word and steady advances for the Library. As committee chairman, now for nearly four decades (since 1958), I must confess to my own increasingly small part in the real operations. Fortunately for us all, there has been a succession of excellent people at the library, all employees of the University of Michigan Museum of Zoology, to carry the load—and, most especially, for many years now, the indefatigable Janet Hinshaw, who I trust will remain in charge for many more years to come. With this report, it is time for me to step down. The "ravages of time" are accumulating, and the committee chairmanship certainly stands to gain from some fresh energy and ideas. I have greatly enjoyed these many years, which seem all too short.

It is obvious that the J. V. T. Library, like all other progressive organizations today, is getting more and more into the computer era. All the record-keeping can be facilitated, and all lists and figures kept potentially up to date and always accurate—but people still have to do it. In addition, Janet has been devoting a lot of time and thought to our growing "web page" (http://www.ummz.lsa.umich.edu/birds/wos.html). Being added to the growing body of information are such embellishments as portraits and appropriate art work. There seems no limit, and only time can tell how extensive will be our contacts, and with what varied audiences. Appreciation is due again to Maricel Fuentes for her period of yeoman secretarial help. At present, she is being replaced as Bird Division Secretary by Joann Constantinides; there is much to learn and much to do.

The following itemized list of transactions for 1997, under our customary headings shows perhaps some small drop-off from recent years.

Donations were received from 14 members: Academic Press (through a request from E. Urban), C. Blem, C. Braun, E. Greij (for *Birder's World*), J. Hinshaw, D. Klem, M. Kielb, L. Kiff (for The Peregrine Fund), T. Nowicki, J. Pinowski, S. Sealy, J. Spendelow, C. Swift, and R. Whiting. These totaled 15 books, 781 journal issues, 709 reprints, and 4 dissertations. In addition, a bequest from Helen Lapham contained approximately 860 books, and 12 boxes of journals and reprints.

Trades with other institutions involved: 3 volumes of *The Auk* to Jan Pinowsky, Institute of Ecology in Poland, for a book; and 7 books to The Peregrine Fund for various publications.

Library Loans: 80 transactions to 57 people, made up of 275 items, including photocopies.

Publications Received: totaled 210 titles from 175 organizations and individuals. These figures include exchanges of 158 journals and reprints, from 123 organizations; subscriptions to 28 titles, from 22 organizations and outright gifts of 34 titles, from 30 individuals and organizations.

Books and Other Items Sold: included 9 books and 415 journal issues, and brought in $499.00.

Purchases of items desired by our library (from the rotating New Book Fund): included 1 book, 1 dissertation, current regular subscriptions, and appropriate back issues under 9 titles, for a total of $501.12.

Only when all these transactions, and their cash values, are considered together, and over a period of years, does it become apparent how worthwhile the Library activities have become—not only from the standpoints of the Society and of its participating members, but in a much broader view, in relation to

ornithology the world over. The Committee appreciates all that is being done, by all parties, and continues to encourage a greater total effort by the membership. Every bit helps!

William A. Lunk, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The mission of the Committee on Undergraduate Outreach is to stimulate an interest in ornithology among undergraduate students, and to help to maintain and focus that interest so as to stimulate students to continue studies in ornithology. The Committee explores ways to increase interest in ornithology both as a focus for future postgraduate studies, and as an avocation for those in fields other than the biological sciences. Members of the committee during 1997–98 are, alphabetically: Albert R. (Jay) Buckelew, Jr., Department of Biology, Bethany College, Bethany, WV; Edward H. Burtt, Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH; Dale Kennedy, Biology Department, Albion College, Albion, MI; Lynn A. Mahaffy, Randolph-Macon College, Ashland, VA; Ernest J. Willoughby, Department of Biology, St. Mary's College of Maryland; and W. Herbert Wilson, Department of Biology, Colby College, Waterville, ME.

From April 1997 through February 1998 the Committee on Undergraduate Outreach engaged in the following activities:

1. With the help of Janet Hinshaw, the "Guide to Graduate Programs in Ornithology" is now posted on the WOS web page. The Committee is in the process of gathering additions and revisions, and plans to update the document at least once a year.
2. Drs. Burtt and Wilson have revised their report on the survey of undergraduate ornithology courses in North America, and submitted it to editor Robert Beason for consideration for publication in *The Wilson Bulletin*. This paper grew out of a project that began as a survey of undergraduate ornithology courses in North America done in 1993 and presented as part of the "Symposium on Undergraduate Outreach" at the meeting in Guelph, Ontario.
3. Dr. Burtt has organized another workshop on teaching undergraduate ornithology. Its title is "Management of Ornithological Collections at Teaching Institutions and Nature Centers," which is to be presented during this annual meeting.
4. Dr. Burtt has compiled laboratory exercises that were presented during teaching workshops at the previous two annual meetings, and with John Faaborg is editing these for publication as an undergraduate ornithology laboratory manual.
5. Dr. Buckelew continues to monitor changing regulations governing salvage of bird skins for teaching collections.
6. Drs. Kennedy and Mahaffy are investigating issues relating to making and lending videotaped interviews with eminent ornithologists for educational purposes.

Ernest Willoughby, *Chair*

REPORT OF THE CONSERVATION COMMITTEE

The Scope and Weaknesses of CITES in Protecting Endangered Birds

Just as the Endangered Species Act of 1973 is the national "law of the land" that protects endangered species in the United States, CITES is the world-wide "law of the land" that we often look to to provide protection for endangered species around the world. CITES, an acronym for the Convention on International Trade in Endangered Species, is an international treaty which was drawn up under United Nations sponsorship in 1973. CITES came into force in 1975 when the United States and 17 other nations became parties to it. As of January 1, 1998, 143 of the world's nations have agreed to its provisions. CITES lists endangered plant and animal species in two "Appendices." Appendix I species are those threatened with extinction. Appendix II species include ones not necessarily yet in danger of extinction, but ones that could easily become so unless trade is strictly regulated. Species similar to critically threatened species are included in these appendices solely because of that similarity as a precaution to protect their troubled look-alikes. A third Appendix also lists species of concern at the request of individual nations, but species on this list are not considered "endangered"; rather they are ones the listing nations want to exercise more local control over.

As an accessory to CITES, in 1976, IUCN-The World Conservation Union established TRAFFIC (Trade Records Analysis of Flora and Fauna in Commerce) to monitor and report on world-wide trade in wild plants and animals. Thus, CITES provides the framework for international cooperation in stemming illegal trade in endangered species, and TRAFFIC monitors both legal and illegal trade, essentially providing an early warning system for excessive trade and data which can be used to bring sanctions against those who do not comply with CITES.

Very importantly, CITES, as an international legal tool, is limited in its scope to international trade in endangered species. As an international law protecting endangered species, CITES has many problems, including the following which I summarize here.

1. Listing of a species on Appendix I of CITES has sometimes driven up black-market prices, encouraging more poaching and "stockpiling" of endangered birds such as Hyacinth Macaws.
2. CITES has no enforcement authority; enforcement of the treaty depends on passage and enforcement of laws by each party nation.
3. Decisions as to whether a species should be listed or removed from Appendix I or II are made on the

basis of both political and scientific information—not necessarily on the basis of the best biology.

4. CITES focuses on international trade, whereas a considerable trade goes on within nations.
5. Habitat destruction and other factors resulting in species losses are not considered by CITES.
6. Listing of a species on Appendix I for some populations and on Appendix II for other populations encourages "laundering" of individuals from the endangered population through labeling them as being from the less threatened population.
7. Trade in parts of animals creates many problems because of the inability of officials to distinguish parts of an endangered species from parts of a non-endangered species. This is relevant for birds in that there is a considerable trade in viable eggs of endangered birds and it is difficult to impossible for unhatched eggs of some endangered parrots, for example, to be identified to species by authorities at border crossings.

The future role of CITES in protecting endangered species is heavily debated within the conservation and scientific communities. Organizations such as the Humane Society International argue that by its very nature CITES promotes trade in endangered species, while others such as the World Wildlife Fund argue that CITES places too much emphasis on limiting trade and not enough on promoting it.

We are at a crossroads today in dealing with endangered species on an international level. More of the world has joined in the paper battle to protect endangered species, but getting meaningful actions is becoming more complex. We need a global legal platform for protecting species from habitat loss and a host of other problems, but can't even agree on how to stem illegal international trade. Two very different approaches are proposed for protecting endangered species from illegal international trade.

One, championed by the World Wildlife Fund and IUCN, would legalize trade as a way to deter illegal trade and to conserve the species. One proponent of trade defined conservation as "the saving of living natural resources for use," arguing essentially that species should "pay their own way." Trade is the "carrot" that is supposed to entice people to voluntarily want to protect the resource.

An alternative, championed by the Humane Society International, seeks to protect endangered species from use. Advocates of this approach argue that if any trade is allowed, illegal trade would be impossible to control. A non-avian example supports this view. In 1997, lifting of the ban on international trade in ivory was anticipated and there was an immediate and substantial increase in poaching of elephants.

One of the buzz concepts of our era is "sustainable use," yet we do not have even the most rudimentary understanding of the nature of interactions between and among most species and their natural environments. Non-consumptive uses, such as eco-tourism and wildlife photography, can benefit endangered species and foster the protection of their habitats, but these do not offer the high short-term economic potential of consumptive exploitation. The international protection of endangered species by CITES or any other agreement among nations is not merely a conservation problem, but a host of economic and ethical problems linked to human population growth and standard of living. We are among the "haves"—having destroyed or drastically altered much of the natural environment of North America to gain the lifestyle we enjoy. The greatest biodiversity in the world lies in the custody of the "have nots"—who have difficulty understanding why they shouldn't follow our example of exploitation.

The answers are not easy, but clearly education and understanding are essential. In the arena of international trade, the purview of CITES, one lesson might be gained from the feather trade of a century ago. In the late 1800s, the feathers of herons and egrets were sometimes worth more than their weight in gold as adornments for ladies hats. Poaching was rampant when laws were passed to regulate hunting, leading to the near extinction of some species. Only through education and changing the attitudes of the common man were we able to bring about enforceable local and national laws and international treaties. When feathers were no longer in vogue, there was no longer a demand, and there was no longer a trade.

The problems are complex and the potential speed of change in a species population has been enhanced by technology. There is hope for many endangered birds, but hard decisions—perhaps different ones for different species—must be made. In the international arena we have political and cultural, as well as ecological, bridges to cross to protect endangered birds. In short, CITES is a very narrow path leading to those bridges and unless its scope is broadened we may not always find our way.

Jerome A. Jackson, *Chair*

The list of papers and posters presented at the meeting and the list of those in attendance will be published in a supplement to *The Auk*, volume 115 (1998).

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